On the Emergence of Macroecological Patterns in Meta-Community Models

Über die Entstehung makroökologischer Muster in Meta-Gemeinschaftsmodellen

Zur Erlangung des Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.) genehmigte Dissertation von Michaela Hamm, M.Sc. aus Langen

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Michaela Hamm, Darmstadt, 18.11.2019

Abstract

A recurring question in ecology is how species diversity arises and persists. Theoretical ecology tries to find underlying principles that explain spatial and temporal species diversity. Models are a valuable tool for this endeavour as they allow to study systems in well-known settings and pin down decisive processes that shape diversity.

Consensus on the core mechanisms that shape diversity is achieved, namely an interplay of evolutionary and spatial processes, but many aspects still need to be included in an overarching theory. One aspect often neglected in models for the sake of simplicity is spatial heterogeneity even though heterogeneity is considered a main driver for species diversity. A similar problem exists for trophic structure. Food web theory has successfully reduced the high dimensional complexity of an ecosystem to predator-prey interactions and proven to capture essential features of empirical food webs like fraction of basal, intermediate and top species. Still many models that try to answer which processes shape diversity neglect food web structure.

This work incorporates both aspects, food web structure and spatial heterogeneity, into the model-based examination of species diversity. Two different food web models considering different scales of space and time are studied: First, a meta-food web model on smaller spatial scales with classical population dynamics to examine diversity patterns found in heterogeneous landscapes and particularly at ecotones. The model suggests that the coupling strength between habitats is crucial for the final outcome of species diversity. A hump-shaped diversity-dispersal relation is observed which is enhanced compared to former studies in homogeneous spatial settings. Second, a new evolutionary food web model developed in this work which is employed to study species diversity on large spatial and temporal scales first in homogeneous and then in heterogeneous landscapes. In both settings the model reproduces a set of well-known empirical diversity patterns, namely species-area relationship, range size distribution, similarity decay of diversity with distance as well as lifetime distributions and evolution of species range sizes, but the exact shape of the relations depends on the spatial setting. Trophic levels have major impacts on the dynamics of species in both settings. Basal species have larger ranges and longer lifetimes than species on higher trophic levels. The most striking difference occurs in geographic range size evolution curves. Homogeneous spatial

settings lead to symmetric curves for basal species, whilst in heterogeneous systems these curves become asymmetric.
This work demonstrates that heterogeneity and complex trophic structure must not be neglected and can easily extend existing ecological models. This enhances the usability of such tools in tackling the questions related to the emergence of biodiversity in space and time. The good agreement with many results found in real systems indicates that the models presented here, despite their simplicity, capture the essence of the processes at work in reality. Consequently such models can guide future research direction and help specify empirical testable hypotheses.

Kurzzusammenfassung

Ein wiederkehrendes Thema in der Ökologie ist die Frage nach der Entstehung und dem Erhalt von Artenvielfalt. Die theoretische Ökologie widmet sich der Suche nach grundlegenden Prinzipien, die Artenvielfalt in Raum und Zeit erklären. Modelle sind bei diesem Bemühen von großem Nutzen, da sie es ermöglichen Systeme unter festen Rahmenbedingungen zu untersuchen und die für die Entstehung von Diversität entscheidenden Prozesse zu identifizieren.

Die Interaktion von evolutionären und räumlichen Prozessen bildet die Grundlage aller Mechanismen, die Artenvielfalt ermöglichen, doch viele weitere Aspekte fehlen bisher in einer umfassenden Theorie der Biodiversität. Einer dieser Aspekte ist räumliche Heterogenität. Obwohl dieser Faktor als diversitätsfördernd gilt, verzichten viele Modelle der Einfachheit halber auf die explizite Implementierung von Heterogenität. Ähnlich steht es um die trophische Struktur von Nahrungsnetzen. Die Nahrungsnetztheorie hat erfolgreich die komplexe Struktur von empirischen Ökosystemen auf Räuber-Beute Beziehungen reduziert und gezeigt, dass empirische Strukturen von Nahrungsnetzen, z.b. der Anteil basaler, intermediärer und Top Spezies, erfolgreich reproduziert werden. Trotz dieser Erfolge verzichten viele Modelle auf die Modellierung von Nahrungsnetzen bei der Identifikation von Artenvielfalt fördernden Prozessen. Diese Arbeit widmet sich der Inklusion dieser beiden Aspekte, Nahrungsnetzstruktur und räumlicher Heterogenität, in die modellbasierte Analyse der Entstehung von Artenvielfalt. Dabei kommen zwei verschiedene Modelle auf unterschiedlichen räumlichen und zeitlichen Skalen zum Einsatz. Zuerst wird ein räumlich kleineres Meta-Nahrungsnetz mit Hilfe expliziter Populationsdynamik betrachtet und der Einfluss von räumlicher Heterogenität sowie der Spezialfall von Ökotonen auf die Artenvielfalt untersucht. Dabei zeigt sich, dass die Kopplungsstärke zwischen den Habitaten ausschlaggebend für die beobachtete Diversität ist. Die Diversität aufgetragen über der Kopplungsstärke zeigt einen unimodalen Verlauf, der auch schon in früheren Studien in homogenen Systemen gefunden wurde. Im heterogenen System ist der Verlauf ausgeprägter als in homogenen Systemen. Das zweite Model, welches im Rahmen dieser Arbeit entwickelt wurde, gehört zur Klasse der evolutionären Nahrungsnetzmodelle und erweitert den räumlichen und zeitlichen Horizont. Das Modell reproduziert eine Vielzahl empirisch bekannter Artenvielfaltmuster nämlich SAR, RSD, Arten-Ähnlichkeitsabfall mit der Distanz sowie Lebensdauerverteilungen

und Zeitreihen der geographischen Verbreitung von Spezies. Das trophische Level hat einen entscheidenden Einfluss auf den Verbreitungserfolg von Spezies. Basale Spezies haben es einfacher und verbreiten sich weiter, was sich auch in längeren Lebensdauern äußert. Die besagten Muster werden sowohl in homogenen als auch heterogenen räumlichen Strukturen mit kleinen Unterschieden beobachtet. Der größte Unterschied erscheint in den Zeitreihen der geographischen Verbreitung von Spezies. Diese bestehen aus einer symmetrischen Kurve von An- und Abschwellen der Verbreitung in homogenen Systemen, im heterogenen System wird diese Kurve asymmetrisch mit einer verlängerten Phase des Abschwellens.
Diese Arbeit zeigt, dass trophische Struktur und räumliche Heterogenität nicht vernachlässigt werden dürfen und demonstriert, dass beide Faktoren in bestehende Modellierung eingearbeitet werden können. Daraus entsteht eine breitere Anwendungsmöglichkeit für diese Art von Modellen und die Fragen nach der Entstehung von Artenvielfalt können umfassender untersucht werden. Obgleich seiner Einfachheit, zeigt die gute qualitative Übereinstimmung der Ergebnisse dieses Modells, dass die grundlegenden Prozesse in einer sinnvollen Weise kombiniert wurden. Folglich eignen sich solche Modelle um die Richtung zukünftiger Forschung einzugrenzen und neue Hypothesen zu formulieren, die empirisch getestet werden können.

Contents

1 Introduction

Nature must be considered as a whole if she is to be understood in detail.

Alfred J. Lotka

Biodiversity or species diversity on Earth is a result of the rise and fall of species that has been going on for the last 3.5 billions of years [1]. Extinction has always been part of this dynamics, either intrinsically happening out of the ongoing species turnover or triggered by external events like meteor strikes. The recent century has seen a tremendous increase in extinctions. Present extinction rates have been estimated to be 100 to 1000 times higher than what is scientifically considered as a "normal" extinction rate [2].

Reasons behind this development lie in the extensive exploitation of the planet by humanity. The impact of human activities on our home planet is so immense that some scientists dub the current geological age of the Earth the era of humans or anthropocene [3]. Main drivers in the loss of biodiversity are destruction and fragmentation of habitats to re-use those areas in a human-centred way, e.g. as farmland or for human infrastructure building [4]. Species loss threatens the integrity and functionality of the ecosystems that enables life for all species including humans. Ecosystem services like air filtration or protection from erosion are provided by the interplay of many species. The loss of a large fraction of these species might lead to a collapse of the interaction network and consequently to a failure of ecosystem functions [5].

To give a concrete example, arthropode (containing species groups like insects, spiders, centipeds etc.) diversity has declined by 34% (biomass even 67%) in grass land and by 36% (biomass 41%) in forest samples in the last eleven years in research sites all over Germany [6]. The authors suggest that agricultural activities on a larger scale (landscape level) might drive this loss in grass land, whilst the decline in forest could not be explained [6]. Biomass of flying insects has even been reported to have declined by more than 75 % over the last thirty years in Germany [7]. Insects play a large role in ecosystems both as pollinators and food source for other species like birds [7]. This demonstrates that ecological systems always need to be considered as networks of interacting species that form an entity together.

There exists the will to protect diversity [8], but any suitable management strategy needs to know how the ecosystem of interest works and what factors impact species diversity. A historical example in ecosystem management theory is the "SLOSS" (acronym for *single large or several small*) debate. The debate was about how conservation areas for (endangered) species, e.g. natural reserves, should be designed. Based on the observation that larger areas hold more species, the species-area relationship, and that extinction rates are lower in larger areas it was proposed in the 1970s that reserves should comprise one large continous area [9]. This view was challenged because two distinct areas could in principle hold more species than one large area depending on the overlap of the species' ranges [10]. The debate is still not settled, several aspects have been asserted since which were not included in the original proposal like spatial heterogeneity or resource restrictions, see [11] for an overview. An overall theory on biodiversity and particularly how biodiversity arises in space is therefore desirable not only from a scholarly point of view, but specifically for conservation management in times of high extinction rates. Scientific consensus exists that the combined effects of speciation (emergence of new species trough evolution), dispersal (movement of species in space) and extinction (vanishing of species from the Earth) shape the diversity of species in space [12]. An intrinsic problem that hinders a full synthesis on biodiversity emergence is the large differences in spatial scales that the involved processes cover [13]. Speciation is a local process that might start with a single mutation in the genome of a single individual. It takes generations to form a new species. This new species might broaden its geographic range and disperse to other locations after its emergence. The interaction between species and their competition for resources keeps an intrinsic species turnover going. What remains from this dynamic is a fossil record of traces of extinct species. The species composition of today is a snap shot of this ongoing process. Together with the fossil record ecological patterns can be analysed and used to elucidate underlying processes that cannot easily be disentangled from paleological data. Interestingly, a collection of spatial and temporal (palaeo-)ecological patterns is observed repeatedly over all kind of habitats and species. Those are:

(1) Species abundances are in general small in one spot. Only few species in a local community are very abundant [14].

(2) Species ranges are in general small. Only few species have large geographic ranges [15] which leads to a decline in community similarity with distance [16].

(3) Paleological data shows that geographic range size evolution follows a two-phased shape [17]. As soon as a species is found in the fossil record it starts

to broaden its range up to a maximum range. Afterwards range declines until the species goes extinct.

(4) Lifetime distribution of species found in the fossil record have broad distributions [18].

(5) The number of species increases with area in a characteristic curve (species-area relation) with a power-law relation for intermediate scales [19].

(6) Species composition depends on the environment. A more diverse environment hosts more species than a homogeneous landscape [20].

(7) Environmental edges have a huge impact on species diversity around those edges [21].

Patterns spark a scientist's interest easily because they whisper of an underlying principle that might hold the key to a more fundamental theory on nature. In the last decades a lot of work has been put into the development of models explaining patterns in space [22, 23]. A theory that explains all these observations at once is still missing but certain ingredients have been proposed to lead to the observation of several spatial patterns together, namely a clumped distribution of species in space, a lack of spatial correlation between different species and a skewed species abundance distribution [22]. It is yet unknown why and how these underlying factors arise. A recent theoretical study found those factors in a Lotka-Volterra model at regional community equilibrium [24]. Those studies and theories normally neglect the evolutionary history of the systems and rely on sampling from specific species distributions or assume assembly dynamics from a predefined pool of species, for an example see [24]. Consequently those models cannot make assumptions on palaeoecological patterns coming from the fossil record and cannot explore the relations between temporal and spatial patterns.
Empirically studying the diversity of the biosphere as a whole is obviously too complicated. Even exploring smaller well-known sets of species in well-defined experimental set-ups is time consuming and tedious. To widen the understanding on biodiversity, especially on larger scales, we need to extract generic patterns out of the vast variety of field data and try to come up with a theory that explains the patterns observed. Where field data is not available we can use simulations to detect patterns in an artificial surrounding. The advantage is that every bit of information that was given to the simulation is known, so it is easier to disentangle which mechanisms lead to a given observation. Hopefully those insights help to interpret the real world, the place where not every piece of the "surrounding simulation environment" is known. Models that tackle patterns on large spatial

scales necessarily need to make simplifying assumptions to keep the work solvable as CPU time is constrained to the average lifetime of a PhD student. Unfortunately this often includes neglecting trophic structure in modelling local communities and assuming homogeneous spatial conditions, despite the fact that spatial heterogeneity is assumed to have a crucial impact on species diversity (habitat heterogeneity hypothesis [25]).

This work is dedicated to the two aspects trophic complexity and spatial heterogeneity. We will make use of the rich heritage of food web theory to model local species communities. The first part uses a classical food web model to create trophic community structures [26] in contrast to the second part that uses evolutionary food web models [27–29]. Food web theory has successfully reduced inter-species relations to predator-prey interactions revealing a characteristic intrinsic layered structure within communities. Food web models have been successful tools in studying processes in local communities [30] and in spatially coupled systems of interacting food webs [31–33]. Contemporary computer power allows to go to ever increasing spatial and temporal scales as well as more complex landscapes that allow for heterogeneity. The thesis starts at intermediate spatial scales and ecological timescales in the world of meta-communities. We will then broaden both spatial and temporal scales and enter the world of macroecology and paleobiology when analysing spatio-temporal patterns in evolutionary meta-communities.

This defines the outer scope of the work, whilst the next paragraph gives a more precise preview on content and research questions that served as motivation for this thesis.

We will first explore what impact heterogeneity has on ecological time scales on a meta-community of a few habitats. Chapter 3 can be given the leading research question:

How does the presence of heterogeneity and particularly edges in environmental conditions alter the diversity in food webs coupled by dispersal?
This will reveal that dispersal strength is crucial in determining whether an environmental edge is positive or negative for species diversity. Heterogeneity can support a higher diversity for intermediate dispersal rates, i.e. that are high enough to lead to source-sink dynamics between resource rich and poor areas, but low enough to not synchronise the whole region. This does not include any speciation process. But as we have seen above, speciation is a fundamental ingredient in the understanding of ecological patterns in time. We thus dedicate chapter 4 to the question:

Can we build a trophic model that is capable of including speciation and dispersal and study the joint effect of both processes on large spatial scale, in spite of complex trophic structure locally?
The answer is yes and we will explain in detail what ingredients and assumptions

are taken into the new evolutionary food web model. The model only includes a minimalistic set of parameters and still produces complex network structures with an ongoing turnover of species. Armed with that new tool we tackle the emergence of patterns on large spatial and temporal scales. Consequently, chapter 5 addresses the question:

What macroecological patterns emerge in the new model on large temporal and spatial scales and what impact has the trophic structure?

This chapter is probably the most exciting, because we find several empirically well-documented patterns at once in our simulations. Among other results we find that species tend to have small, clumped ranges and the sampling over all the small ranges leads to a species-area relation with slopes that are also reported in empirical studies. Moreover, range expansion curves can be derived because we are able to simulate over long periods of time. We find that trophic position determines a species' dispersal success and the shape of the range expansion curve as species on higher trophic levels depend crucially on the species in lower trophic layers. Species that are successful in accumulating large ranges also have a longer lifetime. Those results are obtained under the assumption of homogeneous space. This assumption is dropped in the subsequent chapter in which a specific form of heterogeneity is introduced. The analysis of emerging patterns is repeated in order to answer the question:

How robust are the results to changes in the environment, precisely the implementation of a heterogeneous environment?

The findings are twofold. Most patterns are robust against changes in the environment and only show minor quantitative changes, for example the species-area relationships which show that the heterogeneous setting holds more species on an area compared to the homogeneous setting. The range expansion curves look different in the new scenario. Overall an elongated phase of decline is observed, which is particularly strong for basal species. This indicates that heterogeneity should not be neglected in empirical and especially in theoretical studies as it may alter the results and lead to different hypotheses on how diversity emerges.

Chapter 7 summarises the results of the whole thesis. Before diving into specific model descriptions and results, the next chapter will give a brief tour through ecology and evolution to lay the foundations in biological theory that are necessary to understand and evaluate the results presented later.

2 A Brief Tour through Ecology and Evolution (for the Physicist)

Biology as the science of living things is devoted to the manifold of fascinating processes and structures around the various ways that life found to manifest itself. Ecology and evolution as sub-disciplines revolve around species, their interactions and how they come into existence. The number of different species on Earth cannot be pinned down by any means and can only be described as being immense [34]. In this vast zoo of differing and dazzling creatures one is tempted to get lost in the interesting details [35]. Biology and its subdisciplines ecology and evolution aim at discovering underlying principles to gain a broad understanding of the mechanisms that drive the world of living things. This thesis revolves around ecological questions regarding diversity patterns in space and time. What shapes the distribution of species across space? How does a species' range evolve over time? How does trophic interaction alter a species' dispersal success?
The tools to tackle those questions are taken from other disciplines, e.g., physics and mathematics. We will therefore first begin with a brief overview of ecology and evolution to prepare any non-biologist expert reader (e.g. a physicist) for the body of this thesis. We will focus on the biological patterns that we discuss later. We describe what is known empirically on these patterns and the current status of theory on the underlying mechanisms.

2.1 On Ecology

The Earth is inhabited by myriads of species. Estimates on how many species currently live on Earth revolve around ten million [36]. Plants and mammals are among the extensively studied groups of organisms but only comprise a tiny fraction of the total set of life on Earth [37]. Described species of other phyla like bacteria are less well studied and most species will (probably) never be discovered, either because they are extinct before being discovered or because they are very rare. Ecology is about the organisms making up those species and their complex interactions with(in) other species and the abiotic environment. Interactions between species comprise most different relations taking all shades from antagonism, like predator-prey interactions, to mutualism for example in plant-pollinator relations.

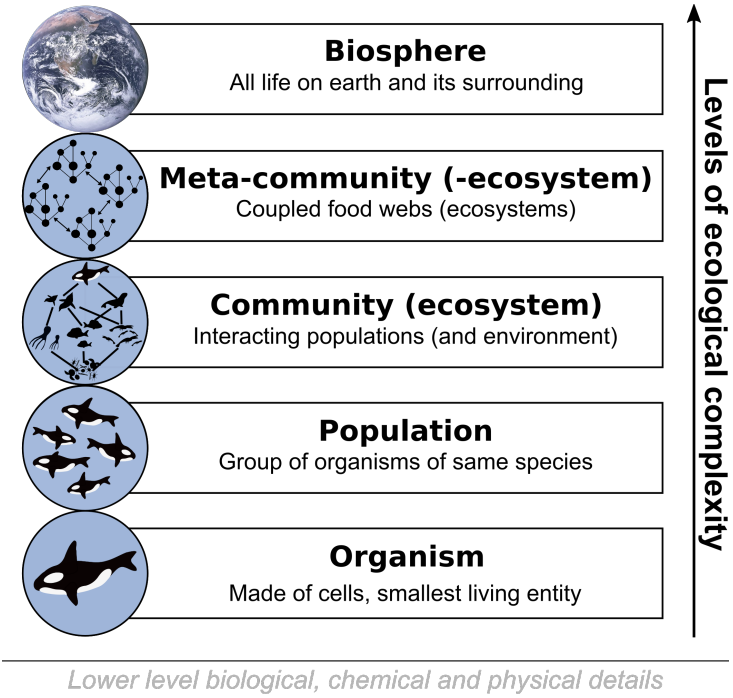

Fig. 2.1: Levels of increasing complexity in ecology. Organisms are the basic ecological unit. Groups of individual organisms of the same species form populations. Populations of different species that share a living environment are called a community or an ecosystem if the abiotic environment is explicitly considered. When space is enlarged and different communities interact they form meta-communities (or meta-ecosystems). The ecosystem comprising the whole globe is called biosphere.

Ecological processes happen on vastly different layers of complexity, see Fig. 2.1. Individual organisms interact on small scales (home ranges) with other individuals, where the size of those ranges already strongly depends on the body size of the species, see [38] for an example on ungulates[1]. Groups of individuals that form populations might already need a description on a different (larger) spatial and temporal scale for example because of dispersal processes (see below). Interacting populations of different species are grouped together to communities and might be described as food webs (see below). If the abiotic environment of a community is also part of the system of interest the resulting structure is called ecosystem. Often, it is a valid assumption to model the environment of a community as homogeneous (e.g. a forest plot or a meadow). Communities can themself interact with other communities by flow of material or energy. Such systems are termed meta-communities or meta-ecosystems. When looking at meta-communities the environment might change (depending on the exact system) from place to place in the area under consideration, be it due to climatic changes or other factors. In that case, the assumption of a homogeneous environment will not be a good approximation any more. When combining all of the Earth's species and their environment into one large interaction network it is called the biosphere. The ecological subfield that is concerned with biological processes on large spatial scales is termed macroecology [39].

The diversity of species, despite the concrete spatial scale considered, is sometimes also called "biodiversity". The term biodiversity is often associated with more than plain species numbers and includes for example ecosystem functions, but this definition is not strict [40]. We will use these terms 'biodiversity' and 'species diversity' synonymously within this thesis.

Ecologists often distinguish between the diversity of a local site under study and the diversity of a larger area that comprises many of those local study sites. Whittaker coined the terms α- and γ-diversity for local and regional diversity, respectively, when he worked on plant diversity in the Siskiyou Mountains [41]. α-diversity is just the number of species in a local community or other assemblage of species, i.e. the number of different species present at one point of interest, e.g., the yield of a light trap. γ-diversity represents the number of all different species in a larger area, e.g., an experimental transect that is made up of n light traps. There is also a third standard measure for quantifying the difference in diversity between two sampling sites, which is called β-diversity. This is defined as the ratio of γ- and α-diversity. A region that is uniform will lead to a β-diversity of 1, whilst a non-uniform region will have a higher β-diversity, i.e., a faster change in species composition. Instead of asking how different two communities are, one can ask how similar they are

[1] Ungulates = hoofed animals

instead. The similarity of two communities can be measured for example by the Jaccard index. The Jaccard index is defined as the number of species that two locations have in common, divided by the number of species in total on these two sites [42]. So if two habitats are identical the Jaccard index is 1, while it is 0 if they have no species in common.

Niche theory

A key question of ecology is how so many species can coexist in one habitat[2]. Each species has certain preferences for a place to live, for example it might only tolerate certain temperature regimes or pH values. Put together, all requirements of a species on its surrounding define its "niche". The term was introduced to ecology by Elton in 1927 to emphasise that certain species fill certain roles in an animal community [43]. In 1957 Hutchinson defined the term more rigorously as an n-dimensional hypervolume in an abstract n-dimensional niche space, where each axis represents a requirement of a species on its environment [44]. Along one axis of the niche space a species' "habitable" zone is often modelled as a bell curve to indicate that the species has a tolerance against some shift in their preferred value of this need, where it might not grow optimally but could in principle persist, see Fig.2.2. In this framework, each species has a potential hypervolume in the niche space in which it could possibly blossom (fundamental niche). If the habitat (the abiotic environment) and the biotic environment, made up by other species in this habitat, match a species' niche it can thrive there. However, as species find a habitat already occupied by other species this might lead to competition between species with similar niches. Competition can prohibit that a species appears in a certain habitat. The niche-space volume that corresponds to the habitats that are really occupied by a species is called the realised niche of this species. As a result of competition or non-matching environmental factors a species' niche, both fundamental and realised, can shift over time[3] [45]. In the limiting case of species that fill *exactly* the same niche one would expect that the species that can utilise the given resources a tiny bit more efficient drives the inferior competitor to extinction. This is called the competitive exclusion principle [46].

The existence of a huge variety of phytoplankton in an environment that was assumed to be very homogeneous raised the question how this could be explained within niche theory. Competitive exclusion should lead to the dominance of the best performing plankton species and reduce diversity. This "paradox of the plankton" [47] stimulated a lot of research. Scheffer et al. summarise the main results that were found to solve the paradox [48]. The most interesting point is that plank-

[2] Habitat terms the abiotic environment a species is found in.

[3] By means of evolutionary processes.

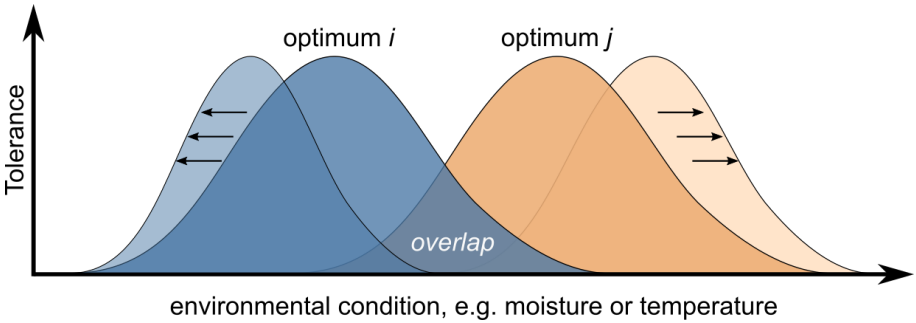

Fig. 2.2: Illustration of the niche concept in ecology freely adapted from [45, p. 181]. The ecological tolerances (niches) against an environmental factor of two species i and j are depicted as two bell-curves. The maxima of the curves indicate that species grow best in these environmental conditions. Where the "niches" overlap species are in competition with each other. Over time this competition can lead to a shift in the niche preferences as indicated by the shifted lighter curves.

ton never reaches equilibrium [48]. Due to species interactions and small-scale disturbances in the ocean, the prerequisite that the plankton community finds itself in a homogeneous and well-mixed state never occurs [48]. Consequently the competitive exclusion principle cannot be applied [48].

The competitive exclusion principle can, however, be tested in experiments. In a plant experiment diversity decreased when initially limited nutrients were added in such a way that they were non-limiting afterwards [49]. The reduced number of limiting resources can be translated into a reduced number of niche axes in the niche theory concept [49]. According to competitive exclusion, the species that can utilise the remaining dimensions of the niche axis best will persist. In case of plants the last remaining niche dimension, when nutrients are non-limiting, is light [49]. We will take up the issue of the influence of heterogeneity on species diversity in chapter 3. For further reading on niche theory we recommend the review of Leibold [50].

Neutral theory

An alternative theory on species diversity and coexistence is the neutral theory proposed by Hubbell almost twenty years ago [23]. Neutral theory abandons all assumptions on niches in an abstract space and assumes that species are identical. However, this is only assumed for species that are on the same trophic position (see

food web section) in an ecosystem, e.g., plants. This is in stark contrast to the prevailing opinion formed by decades of ecological research based on the niche theory and consequently is a highly debated and by many ecologists rejected theory. The reason that neutral theory is still around is at least twofold. First, neutral theory can reproduce a large number of patterns that are observed empirically [51]. Second, it challenges the way one thinks of a problem and stimulates creative and innovative research by encouraging scientists to leave their comfort zone. Wennekes et al. identify in the rejection of neutral theory a representative example of the "instrumentalism versus realism debate" [52]. They infer that ecology has too long focussed on the realism aspect of understanding nature and is used to small scaled models that try to capture as much detail and "truth" as possible. Being used to such thinking patterns makes it hard to accept the more pragmatic approach of the neutral theory that does not claim to capture the fundamental underlying truth (realism), but emphasises the usefulness of the predictive power (instrumentalism). Other authors advocate that niche and neutral theories are not necessarily contradicting, but rather complementary [53], or view the neutral theory as a special case of the niche theory of species with identical fitness [54].

This work focuses on niche based models as it utilises food webs that have a clear trophic structure and thus falls out of the classic scope of neutral models. However, because of their vast impact on ecological research neutral models should be mentioned as an alternative approach.

Dispersal

Spatial ecological patterns emerge from the ability of organisms to move. There exists a large palette of movement possibilities. Small seeds or plankton might just be passively transported by wind or other streams, whilst larger organisms often have specialised locomotion apparatuses like legs or fins. Many species need to roam a territory in the search for food or mating partners. Also common are recurrent movement cycles, e.g., the winter migration of songbirds into warmer regions in the south or the salmon run. Dispersal is defined as the movement of individuals away from their birth place to another place where they will reproduce [55, p. 3]. This leads to interconnection of spatial sites by organism flows. The process of species moving into areas that were formerly not inhabited by this species is termed colonisation. The theory of island biogeography introduced a conceptual framework that explains species diversity on islands by the interplay of colonisation and extinction rates [56]. This theory influences ecological thinking still today. Originally concerned with islands that are some distance away from a mainland, the theory was later applied to all kind of environments that can be described by suitable habitats residing in a matrix of not suitable environment ('ocean'). Species diversity

on an island is the result of how often colonisers arrive at the island (colonisation rate) and how often extinctions on the island happen (extinction rate). In equilibrium these two rates balance each other out and a stable α-diversity is established on the island. The point of equilibrium depends on the area of the island, which is assumed to influence colonisation (higher chances of colonising larger islands) and extinction rates (higher extinction rates on smaller islands because of smaller populations that are more sensitive to environmental fluctuations).

This work only considers systems from the population scale on. Consequently dispersal will not be modelled by individuals moving but rather in such a way that in each dispersal event a fraction of a population leaves a site and disperses into or colonises a neighbouring site. Detailed descriptions of the processes follow in the descriptions of the models used.

Food webs

As sketched above, ecological processes happen on a large range of spatial and temporal scales. When modelling a system to study such processes it is crucial to include the essential parts of a system and leave unimportant details aside.

For the study of ecosystems, food webs have proved to do just that. Food webs simplify species interactions by only including trophic interactions, i.e., information on who eats whom. As predator and prey sets are the only things that matter, species with the same prey and predator sets can be grouped together into "trophic species" [57].

A food web can be illustrated by a graph. Nodes depict species and edges mirror predator-prey interactions in the direction of biomass flow. Figure 2.3 shows an Antarctic food web as an example. The graph of a food web reveals a characteristic structure of food webs: They are layered. Energy for a food web is provided by an external source which could be, for example, solar radiance or just plant biomass, depending on what system is being modelled. The energy flows from bottom (basal species) to top (top species, apex predators) in a food web, passing different layers of intermediate species. The different layers are called trophic levels. There are many possible definitions of trophic level [58]. We use two of them in this thesis. In chapter 3 we define the trophic level as the minimum number of links from a species to the external energy source. In chapter 4 and later we define the trophic level as the average trophic level of all prey species plus one.

A single food web depicts a community at one habitat in space. Coupling several spatially distinct food webs, a so called meta-community or meta-food web, incorporates the spatial aspect. Species can then disperse between adjacent habitats. Space can be modelled as a graph, such that each node hosts a food web. This leads to a "network of networks", a spatial network of trophic networks.

Temporal aspects can be modelled by defining dynamics in the system. For example, trophic interactions can be modelled by population dynamics like the Lotka-Volterra equations [59]. Evolutionary dynamics can also be defined as we will demonstrate in chapter 4, but because of time scales much larger than for trophic interactions, assumptions must be made on how trophic and evolutionary dynamics interact and the use of population dynamics is uncommon.
We will first use a meta-food web model without evolutionary aspect to study the influence of heterogeneous space in detail in chapter 3. We model population dynamics by a set of coupled differential equations. This gives detailed knowledge of the time evolution of biomass densities of all species in the food web. Chapter 4 introduces a evolutionary food web model that replaces population dynamics by a simpler self-consistent equation and defines evolutionary dynamics. We then analyse the combined effect of evolution and dispersal. Detailed descriptions of the models are presented in the respective chapters.

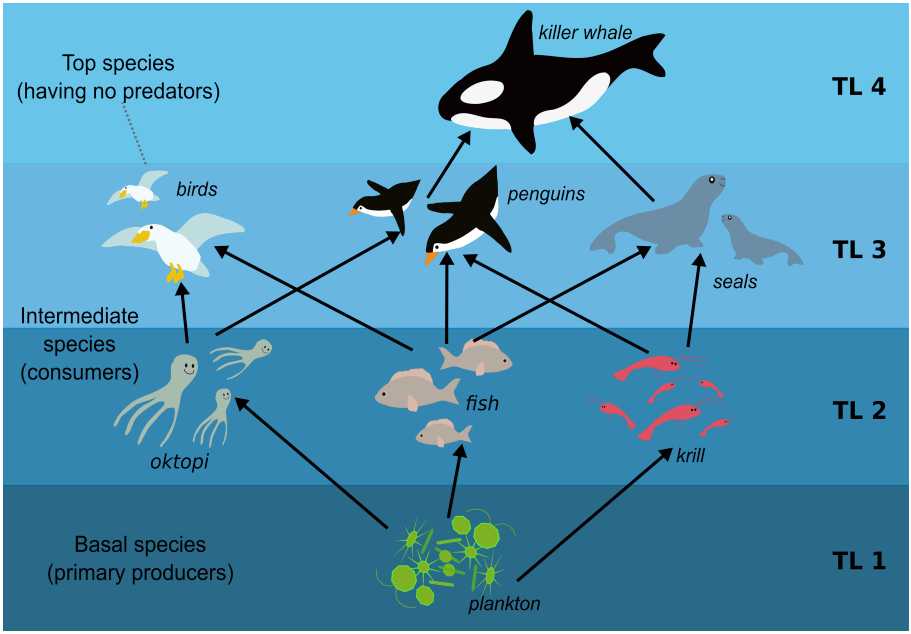

Fig. 2.3: Example food web depicting trophic relations between species inhabiting Antarctica's waters. Sunlight brings energy into the system which is processed into biomass via photosynthesis by primary producers like plankton and other protists. Plankton serves as food for the next trophic layer consisting of species like krill (crustacea) and fish. Those species are themselves prey for the next level of larger species like seals and penguins. The apex or top predators feed on those larger animals and have no predators.

2.2 On Evolution

Evolution studies how species come into existence by descending from other species and eventually vanish again. The publication of Darwin's "On the origin of species" [60] laid the foundation for modern evolutionary biology.

The next paragraph briefly sketches the process that leads to new species: Speciation. We will not dive into genetic details here, because the models we discuss later work on a higher level of abstraction. As extinction is a fate that awaits each and every species we will also describe extinction and the theories around it.

Speciation

The definition of species is not straight forward and there are lots of (slightly) different definitions [61]. They all focus on something that a set of organisms do share (same species) or do not share (different spcies). This might be for example morphological traits, genes or behaviour. For example, later in this work species will be defined by their body mass and the range of body masses that they can prey on. Species evolve gradually from older species. There is a distinction between the gradual change of a species as a whole - anagenesis, and the branching of a new species from an old one - cladogenesis. Throughout this thesis we will mean cladogenesis when talking of speciation. The difficulty in grasping speciation is the entanglement of different scales. The genetic information is stored in genes residing in individual organisms. Mutations in the genetic code give rise to genetic variation in a population. Natural selection works on groups of species filtering out the "fit" individuals that can inherit their genomes. Mayr summarizes this as follows: "It is important to emphasize that *all macroevolutionary processes take place in populations and in the genotypes of individuals, and are thus simultaneously microevolutionary processes.*" [62]. For this work a detailed knowledge of the micro- and macroevolutionary processes is not needed, wholesome descriptions are found in the literature, for example, [62]. The speciation process of a particular species can be reconstructed by aligning fossils from different geological ages. There are remarkable examples of lineages that are known to a very fine detail. For example the lineage of whales (Cetacea), that descended from terrestrial even-toed ungulates (Artiodactyla) just like the hippopotamus which makes the hippo the closest related living sibling species of the whales [63, 64].

Extinction

One of the most striking observations that comes from the fossil record is that most species are extinct. This might seem trivial to a contemporary human, but this observation did need time to trickle through minds. Yule for example, who

developed a model for cladogenesis in 1925, writes: “It seems doubtful, at the least, whether we have any reason to predicate death as normal for a species in the same sense that it may be normal for one of the higher plants or the higher animals.” [65]. For him extinction was mere the result of an “cataclysmic” abiotic event, e.g., a glacial epoch or climate change, and not the expected fate of a species. In the recently published “Five laws of paleobiology” extinction is specifically mentioned as the first law [66]. This states that lineages become extinct. One can even derive the rate of extinction by extracting the number of extinct species (often not on species level but higher taxonomic order, like families or genera) per geological strata from fossil record data. This rate is called “background extinction rate” or normal extinction rate. The background extinction rate is roughly constant over time [18], or at least was until the beginning of the anthropocene, which we will discuss at the end of the chapter [67].
Mass extinctions stand out of the constant background extinction rate as peaks of high extinction rates [68]. They mark phases of major biotic changes. Often new geological ages coincide with mass extinctions as life is coupled to the environment. Current scientific consent is that mass extinctions are driven by abiotic factors such as climate change. For example, the meteorite impact that caused the mass extinction at the end of the Cretaceous (extinction of the dinosaurs) was followed by a cooling of the earth. So far five mass extinction events (‘the big five’) were found to be documented in the fossil record, that each erased more than 75% of all living species [68]. Because of an accelerated loss of species, it is discussed if the present status of the earth has to be considered as a phase of a sixth mass extinction [67]. After such a radical event like a mass extinction a short period of a burst of speciation follows [69]. A lot of niches are completely free and life starts to claim them back, creating new and different ecosystems [69].

The Red Queen Hypothesis

Van Valen formulated the “Red Queen Hypothesis” after he found that the age of a species does not influence its chance of survival [70]. This is counter intuitive as one would expect that a species that already managed to survive for some time might have some traits that are especially advantageous. Van Valen reasoned that species evolve together such that no species ever gains an advantage over the others and in turn cannot reduce its chance of becoming extinct. This is also called the “law of constant extinction”. The influence of large geographic ranges on extinction probability challenged the Red Queen hypothesis [71], but the overall idea of an ongoing co-evolution prevails and keeps stimulating eco-evolutionary thinking [72].

The History of Evolution

Pre-Darwinian Time (before 1859)
Long before Darwin, scientists and philosophers speculated about species evolving or at least being created somehow, but these ideas were not elaborate enough to count as theories. The most often cited pre-Darwinian theory on evolution was proposed by Lamarck (1809). He explained that a subsequent use of skills or organs will emphasize them in an individual, which in turn can give those obtained traits to its children.

Charles Darwin
The theory on evolution introduced by Darwin in 1859 [60] (after contemplating it for 20 years before publishing) has accumulated so much scientific proof that no scientist will reject it [62]. By studying sub-species, like the famous finches on the Galapagos islands, Darwin concluded that species developed from a common ancestor by natural selection, i.e., individuals that better fit their environment will have higher reproduction success and pass on the traits that make them adapted to their offspring.

The Modern Synthesis
The rediscovery of the genetic experiments by Gregor Mendel after Darwin's publication allowed evolutionary thinking to flourish further. Darwin had proposed natural selection *selects* individuals with fitting traits, but this machinery could only work if there was variation between individuals. The inheritance experiments suggested that variation can be found in the mixing of parental genes when they are passed to the following generation. However, one must not forget that natural selection works on the phenotype of an individual. This name of this 'era' stems from the book title "The modern synthesis" by Julian Huxley, in which he synthesises evolutionary theory in 1942 [73].

The Extended Synthesis (2008)
The time in between the modern synthesis and the current millennium brought new insights from genetics, population ecology etc. such that some authors pledged for a renewal of the synthesis on evolution. "The extended synthesis" emphasises topics like epigenetics (inheritable traits that are not caused by a change in DNA, but changes on the outside of the DNA) or niche construction (individuals shape their environment/niche and are not just at the mercy of their environment) [74].

2.3 Ecological Patterns in Space and Time

The search for "fundamental laws" or "unified theories" is a recurrent theme in ecology [22, 75]. Two examples are normally quoted for biology: Evolution [60, 62] and the metabolic theory [76, 77]. However, it is hard to find ecological laws comparable to fundamental physical laws like thermodynamics or Newton's axioms. Lawton summarizes this as: "parts of science, areas of physics for instance, have deep universal laws, and ecology is deeply envious because it does not" [35]. Recurrent problems of fundamental theories in ecology are the different scales on which ecology happens [13] and the fact that individuals interact with each other in a plenitude of different ways [35] unlike particles in physics for example. Nevertheless ecology has discovered a set of patterns that have some predictive power [78].

This section is designed as a collection of empirical patterns of species diversity. We will start with patterns in space and go from smaller to larger spatial scales to point out which patterns of biodiversity are known empirically. As time and space are interconnected, we will then turn to patterns that emerge over time as a result of dynamic processes.

Empirical Diversity Patterns in Space

Species abundance distribution

Starting on the smallest spatial scale - a point in space - we can already find one of the most omnipresent ecological patterns. It was described as early as 1928 as Williams reports in his book on ecological patterns [79], referring to an unpublished thesis, but was probably long before recognised though not scientifically explored [79]. How does this pattern look like? When one sets up a trap, say a light trap for studying the moth diversity in the front yard, the diversity of insects caught will first of all depend on how long the ambitious scientist samples (i.e., waits). When counting not only the different species but also the number of individuals per species accumulated in the sample one obtains the species abundance distribution (SAD) for that front yard. The shape of this distribution will show that a few species are very abundant whilst most species are only represented by a few individuals, see panel a in Fig. 2.4. This is what is often abbreviated as "most species are rare" [80]. When sorted for occurrence - the more abundant a species is the more to the left it occurs in the plot - one obtains the so called "rank abundance curve" (RAC). With arithmetic scaling the RAC resembles a "hollow curve" because of the small number of common species. This pattern is so ubiquitous that it is labelled as one of ecology's few universal laws [14], though it is rather a uni-

versal observation or pattern. It is observed over and over again in all taxa, e.g. snakes [81], birds [82] and plants [83], for a meta-study see [84].

There is an ongoing discussion which functional form describes the SAD best as well as a plethora of theoretical ideas trying to explain the SAD pattern. Two promising candidates are the log-normal and the exponential function, see [85] for comparison of different functions. A good review on SADs is provided by McGill [14]. One explanation is particularly close to the niche theory and models of this type are called "niche apportionment" models. Imagine all the resources of a habitat stringed on a line in a habitat that is initially not occupied by any species. An incoming species will allocate some resources, based on its niche requirements and thus reduce the amount of resources remaining. The next species will allocate resources from the remaining part thus making the remnants even smaller. This repeats until no resources are left to support further species. Because resources are distributed like breaking pieces apart for each species it is also called a "broken stick" model [82]. Depending on the fraction of resources allocated per species (e.g. half, third or an arbitrary fraction) one can calculate a theoretical SAD and find shapes that look very empirical, see [86] for comparison of different models.

Range size distribution and decay of similarity

A similar pattern like the SAD emerges when looking at the range size distributions (RSD). Range denotes the size of the area that a species appears in. The main observation is that ranges are typically small, so the "most species are rare" observations translates into the "most ranges are small" observation in terms of geographic range [87]. Even the same functional forms are discussed as in the SAD case (log-normal, logarithmic) [88, 89]. This observation has direct implications on diversity in space. If species mostly occur in small local ranges, this in turn means that species composition should change (rapidly) with distance, see panel b Fig. 2.4. The resulting pattern is called the distance decay of similarity [16]. Nekola [16] formulates the consequences quite philosophical: "The distance decay paradigm suggests a natural world that is, at some scales, everywhere unique." Similarity decay with distance is most often reported to follow an exponential decrease [16, 90]. At least two explanations exist for this observation: the niche difference model and the model of temporal and spatial constraint [16]. The niche difference model is the application of niche theory on geographic spatial scales. Environmental changes occur in all kinds of parameters that are mapped to requirements in the niche space of species. Thus species with different niches sort along an environmental gradient leading to a gradual decrease of similarity (species sorting). The second model emphasises the impact of the spatial topology on dispersal success of species. Different species will experience the same envi-

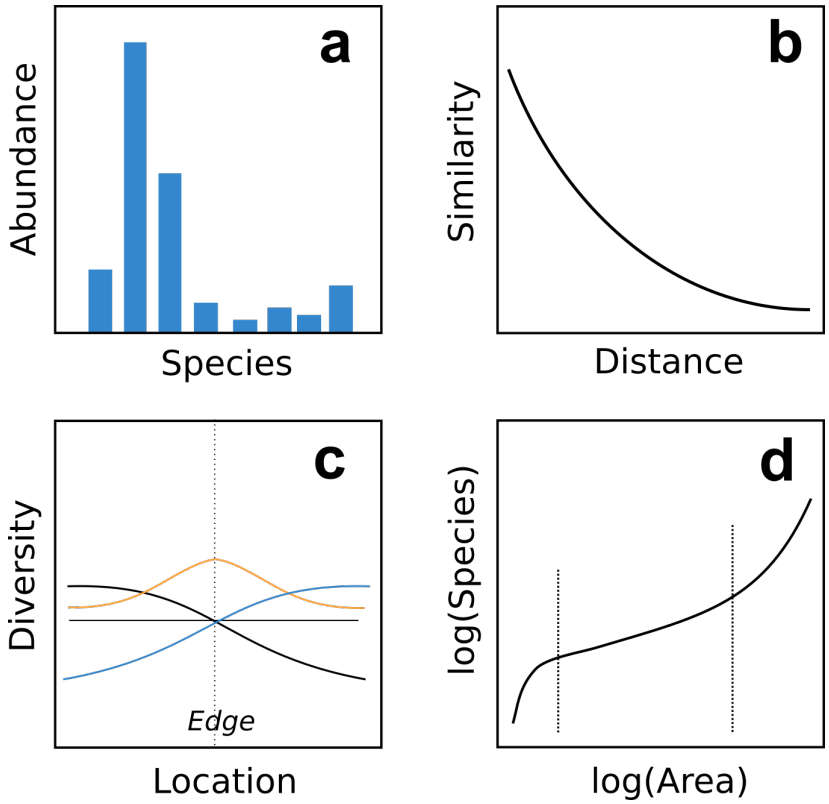

Fig. 2.4: Sketches of empirical patterns of diversity in space. **a**: Species abundance distribution illustrating the "most species are rare" observation. **b**: Similarity decay with distance. When comparing species of two separate locations the chances of finding the same set of species decreases with distance. This leads to species-area curves, see d. **c**: Edge effects. Crossing a border between distinct habitat types might lead to different diversity curves at the edge from positive, neutral to negative effects. **d**: Larger areas contain more species. Species have only a limited range that they live in (see also b) as soon as one starts to go to ranges larger than that one will discover new species each time the area is increased. Local, regional and continental scale are indicated by dotted lines. The regional scale can be described by a power law.

ronment differently depending on their dispersal abilities. The landscape might present dispersal barriers for species so that an instantaneous species sorting is not possible. The species composition will thus depend on the spatio-temporal history of the landscape. But even in (theoretical) homogeneous landscapes one expects a decay in similarity because species have a limited dispersal speed [23]. In complex real world ecosystems all effects will be intertwined and work together to shape the decay curve [90]. A metastudy on similarity decay over all kind of systems showed that the decay rate depends on trophic level. Species on higher trophic levels have higher decay rates for similarity [90].

Edge Effects

The decay of similarity is observed as a trend when comparing communities far away from each other. This naturally neglects diversity patterns on small spatial scales. But what if we "zoom in" and analyse species diversity at a landscape border let's say from meadow to forest? Are there small scale diversity patterns at those edge regions? The area between habitats of distinct types is also called ecotone[4] [91]. We will use both terms - ecotone and edge - synonymously throughout this work. Ecotones arise naturally whenever the habitat type changes. The "sharpness" of the change can vary and might be described by landscape contrast [92]. With increasing habitat destruction and degradation the amount of edges increases due to human activities. The impact of edges on biodiversity is thus of high interest for conservation and wildlife management. As easy as the definition of an ecotone seems, the harder it is to identify ecotones in real world systems. Though there is the quest for objectively defining ecotones in nature [93] ecotones strongly depend on taxa, landscape type and research question. An ornithologist for example will not be interested in an ecotone of high and low pH soil, as long as this does not lead to an ecotone in trees that are used as nesting sites for the birds under study, whilst a research focussing on soil organisms will be highly interested in pH gradients or soil ventilation [94]. There were multiple research reports on all kind of edge response patterns, see Fig. 2.4c. The essence is that edges do not show such clear and ubiquitous patterns like the SAD or the decay of similarity. Edge effects are mainly driven by small scale processes that are unique to the species that participate and are highly dependent on the details and traits those species have. Nevertheless we list them in the pattern section because a simple theoretical framework exists that explains a large variety of edge patterns [21]. This will be discussed in detail in chapter 3.

[4] The terminus was originally introduced for edges between areas of different vegetation but became a common term for all kind of edges.

Species-Area Relationships

When one counts the number of different species in an area, the outcome of this counting depends on the size of the area under consideration. Larger areas hold more species. This relation, the species-area relationship (SAR), is one of the best studied relations in ecology, even dubbed "one of community ecology's few genuine laws" [95]. There are two major hypotheses on why the number of species increases with area [96]. One is the habitat heterogeneity hypothesis that assumes that larger space will inevitably be more heterogeneous and thus provide more niches for species to occupy. The other originates from the theory of island biogeography and emphasises the interplay of extinction and immigration rates. The idea is that small areas should hold smaller populations and have an increased extinction rate, because small populations are more prone to fluctuations. At the same time small areas have lower immigration rates because the chance is smaller to hit a small area than a large one. Larger areas in turn can support larger populations and have smaller extinction rates as well as higher immigration rates. This should lead to more species in larger areas in case of equilibrium, see [96] and references therein. An alternative explanation lies in the simple sampling from an underlying species distribution like a log-normal or logarithmic SAD [97, 98].

The form of the curve when species number is plotted against area shows a characteristic increase. The two repeatedly reported functional forms of the SAR are exponential and power law like, but the power law is the dominant and best fitting form [19]. A power law will relate the number of different species S in an area A over

$$S(A) = cA^z. \tag{2.1}$$

In a log-log plot this will lead to a straight line with slope z and intercept $\log(c)$. SAR curves were reported for almost all taxa, e.g. birds ($z = 0.227$) [99], mammals ($z = 0.18$) [100], or even soil microbes ($z = 0.2$) [101]. The average value for the exponent lies around 0.27 as reported in a metastudy [19]. Detailed evaluation resolves that the SAR has a tri-phasic shape: Local, regional and continental scale [23, 51, 102], see also Fig. 2.4b. The local scale happens on the level of individuals and thus shows a steep increase with area until the local community has been sampled. The regional scale is where the power law like shape is observed. In this regime the species composition is determined by the overlap of species geographic ranges [95] that are in the order of the sampled area. The continental scale refers to sampling areas that are so large that species ranges are typically smaller. Consequently, completely different communities are comprised in such large areas and the slope of the power law converges to 1. Theoretical studies show that the slope of the power law decreases with increased dispersal rates, because this

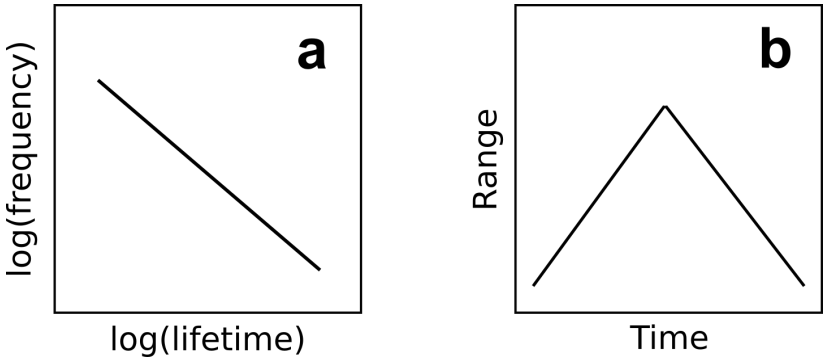

Fig. 2.5: Sketches of empirical ecological patterns in time. **a**: Frequency, i.e., fraction of species that appear for a certain time in the fossil record. This time is denoted as the lifetime of a species. Lifetime distributions are very broad. They might follow a power-law or an exponential function. **b**: Evolution of a species range over time follow a triangular shape. After emergence of the species the range is increased in a phase of waxing. As soon as the maximum range is reached a phase of waning follows and the range declines until the species is extinct.

leads to a homogenisation of neighbouring communities, e.g., [103]. Several sampling methods for SAR exist and there are systematic differences in the slopes, for example, when sampling in a nested way or sampling whole islands [95].

Empirical Patterns in Time - Evolution's Foot Print

The fossil record is a window into the past that gives us a hint on how life on earth looked millions or even billions of years ago. Besides observing living species it is the only possibility of studying evolution [66]. But there is more to it than just the reconstruction of phylogenetic lineages. One must keep in mind that the fossil record is not complete [104]. The chances of getting fossilised depend on the structure of the species as well as their surrounding (tar, sand etc.). Soft tissue like skin and muscles are seldom preserved, whilst bones and shells have better chances of getting fossilised. Another aspect is the size of organisms. Larger organisms have higher chances of getting disrupted or only partly conserved in contrast small organisms might easily be preserved in one piece. The older the fossils the higher the chances that geological processes like plate tectonics destroy them. Unsurprisingly a whole subdiscipline of palaeontology is concerned with taphonomy,

i.e., the processes leading to fossilisation. A review on that topic is given in [105]. This biases the fossil record towards smaller organisms that contain a lot of carbonised elements, e.g., snails, ammonites and other small marine organisms. With this in mind, we discuss two patterns that occur from the fossil record: Lifetime distributions and species geographic range evolution curves.

Lifetime distributions

As species eventually go extinct their lifetime is trivially limited. The lifetime distributions of extinct species has long been recognised to show a recurrent pattern across all types of genera [18]. Lifetime distributions are typically broad with decreasing number of species living for a very long time, c.f. Fig. 2.5a. Even today it is not clear if an exponential or a power-function resembles the data better [106]. In case of a power law for long lifetimes the exponent is pinned down to be in the range of -1.6 [18]. McPeek suggests that the large differences in species lifetimes arise from a distinction between coexisting and transient species from studying a speciation model on an environmental gradient [107]. Coexisting species are species that will infinitely long coexist in their biotic and abiotic environment, assuming this stays constant. Transient species are species that are inferior competitors and therefore will inevitably run into extinction after some period of time. The length of this time span (the lifetime of this species) depends on how similar a species is to its competitors. This is the application of the niche theory and competitive exclusion principle on palaeological time scales. Species that are very alike can spend a longer time in the transient phase because their performances are almost equal and consequently the inferior competitor lasts longer. The number of coexisting species is assumed to increase if species variation in ecological performance increases (i.e., species' niches overlap less) [107]. In the extreme case of neutral species (dropping the niche idea) all species would be transient species and lifetimes be elongated (infinite for real neutral species) compared to lifetimes in a niche based approach [107].

Geographic range evolution

As species develop locally and must disperse from their cradle of birth into the surrounding environment the geographic range size (i.e., the size of the area where the species can be found) evolution might be captured in fossil data. If there is a pattern observed in range size over time this means that age of a species and range size might be correlated (age and area hypothesis [108]). A decline in range size might then be used to predict the extinction risk of a species. This contradicts the assumption of the Red Queen hypothesis that extinction risk is independent of species age. To resolve geographic range size adequately data sets

of high quality, especially of high temporal resolution are necessary. Several range expansion patterns could in principle be possible from a symmetric waxing and waning to asymmetric curves of slow/fast increase to fast/slow decrease or patterns that remind of random walks [109]. Recent synthesis expects geographic range expansion to be a symmetric [110], "hat-shaped" [111], triangular curve, i.e., a steady increase in range right after coming to existence up to a point of maximum range followed by a steady decrease in range up to extinction [17], see Fig. 2.5b. Foote et al. found that area and lifetime play even roles in shaping the range expansion curve: Longer lifetimes allow for larger ranges and larger ranges buffer local unfavourable conditions that might lead to extinction [104]. Zliobaite et al. found that the "tip of the hat", i.e. the maximum range size, is stronger influenced by competition whereas the flanks of the curve are affected by environmental factors [111].

Theory on range size evolution revolves around the joint impact of niches, heterogeneous environments and dispersal [112], similar to the theory of range size distribution [113].

So far, there is no consensus on what exactly determines the shape of the geographic range time series [113]. The recurrent finding of triangular shaped curves suggest that there might be an underlying systematic process that is not yet identified.

2.4 Human Impact on Biodiversity

Humans have settled in all biomes of the Earth and changed landscapes to match their needs. There are even scientists that propose to call the current geological age the "Anthropocene" - the era of humans, because the human foot print on Earth is so immense. A historical review is presented in [3]. A review on human land use reports that around half of the earth's surface has already seen degradation and a quarter probably already suffers a decline in ecosystem functions, see [4] and references therein. Consequently, the large fraction of the Earth's surface that is more or less exclusively used by humans cannot be considered as natural habitats for species that might have lived in these regions in the absence of humans. In some cases a peaceful coexistence between humans and other species in humanly used regions is possible and some species adapt to the newly created artificial landscapes quite well. To give an example, the kestrel successfully adapted to a life in cities and utilises for example spires and other buildings for nesting instead of trees.

But in principle non-humans lose. The list of human induced extinctions is growing fast. One common reason of extinction in history was hunting, for example, the New Zealand running birds Moas or the famous Dodos [114]. Even today hunting

can be a main threat for species as recently proposed by Kamp et al. who analysed the abundance evolution of the once super-abundant singing bird Yellow-breasted Bunting that is now strongly endangered, probably due to illegal hunting in south-east Asia [115]. Another threat for species diversity is the destruction of habitats [116]. Habitat destruction has multiple causes. One major factor is agriculture. Human population has more than doubled in the last fifty years resulting in an increased demand of human edible food. The nutrition habits of western countries exacerbate this with a high demand on meat products that need large areas for livestock and fodder. But also infrastructure takes space away from the wilderness, be it mining spots, highways or cities for people to live in. War also leaves its trace in landscapes. The Vietnamese war caused the destruction of large parts of Vietnam rainforest due to the use of Agent Orange. What only took a decade to destroy will need centuries to recover [117].
In view of this it is not surprising that extinction rates have seen a dramatic increase in the last decades [2, 118]. Biodiversity loss was taken into the list of nine "planetary boundaries" - which formulate limits for human action to prevent the Earth from running into a state that is potentially disastrous for humanity [5, 119]. The threats that arise from biodiversity loss are twofold. First, ecosystems that depend on complex species interactions provide invaluable ecosystem services for humanity, like CO_2-storage, air filtration, erosion resistance etc. Declining species diversity might lead to a collapse of these functions. Second, diversity in the realm of genes holds a gargantuan potential of adaptation. Genetic diversity might quickly produce species that are better adapted to emerging environments, that are on the rise due to humanity pushing to the other eight planetary boundaries, like climate change and ocean acidification. If this potential is diminished, ecosystems might not be able to adapt to environmental changes as quickly as humanity would need them to. A major challenge against biodiversity loss is the entanglement of biodiversity with all the other boundaries [120]. It it thus of utmost importance to enhance our understanding of biodiversity emergence.

3 Ecotones and Habitat Heterogeneity in Meta-Food Webs

The world is patchy and heterogeneous!

Mouquet et al. [121]

This chapter starts with highlighting major findings on the impact of space on diversity in ecosystems.Many of these results were obtained assuming homogeneous space and/or small spatial scales. On small spatial scales the assumption of homogeneity might be reasonable, but for example at boundaries between biomes heterogeneity cannot be neglected. We were interested in how heterogeneity alters or confirms those findings. We therefore studied a meta-community model in heterogeneous space. Heterogeneity was implemented by a superposition of the spatial network and a heterogeneous resource distribution. This approach allowed us to tackle two aspects of heterogeneous space: (1) The overall effect of the resource distribution on robustness; (2) Effects of edges or ecotones on the robustness of the meta-community. We find that dispersal strength crucially determines if heterogeneity is positively influencing diversity. Intermediate dispersal rates can work as a mediator between regions of high and low resource abundance and lead to an increased diversity, especially at ecotones. The chapter closes with a discussion of the results.
Early ideas of this study were also discussed in [122] and developed further within this work. The results were published together with Barbara Drossel in the article *Habitat Heterogeneity and Edge Effects in Model Metacommunities* in the *Journal of Theoretical Biology* [32].

3.1 Introduction

Species have long been viewed as entities that thrive through space [123] yet food web theory has long studied communities of species as if they were isolated [124]. The reason behind is not that spatial aspects were not recognized, but because ecological processes happen on different spatial, temporal and biological scales [13]. Vastly different scales are inherently difficult to study in one framework.

In the second half of the last century it became clear that dispersal opens completely new dimensions in understanding species diversity. A steady influx of dispersers (that are locally inferior competitors) from the neighbourhood can undermine the competitive exclusion principle and lead to higher diversity than what could be expected from a purely niche based view, a process that is called a 'source-sink' dynamics, for a review see chapter 10 in [121]. This stimulated the development of meta-population theory [125] that describes a species distributed patchily in space. A meta-population consists of several of those local populations that are coupled. Individuals in a local population do interact more with individuals in the same local population than with individuals from other populations because they are spatially separated, see [126] for a review. Meta-community theory extends meta-population theory to more than one species [126]. A special form of meta-communities are meta-foodwebs, that explicitly take trophic structure into account [127]. One key result from meta-community studies is a hump-shaped relationship between local diversity and dispersal strength [127]. Small dispersal rates simply do not couple the habitats strong enough for an effect to be observable, so habitats can be considered uncoupled. Large dispersal rates that couple habitats too strongly lead to a synchronisation of all habitats and, hence, exhibit behaviour which is comparable to that of one large patch. Intermediate dispersal rates lead to higher local diversity. Species that would locally go extinct can be replaced by an influx from other patches. This effect is called rescue effect and was originally formulated for island-mainland systems [128]. Species that become extinct on an island can be rescued by immigrants from the mainland source.

Heterogeneity has been identified as a key actor when it comes to diversity and niche partitioning (as seen in Chapter 2). Yet, in the spirit of simplification, homogeneous space is easier to explore and already gained fruitful insights in the dynamics of ecosystems. However, some outcomes can be surprisingly different if heterogeneity is assumed. For example, Amarasekare and Nisbet [129] found in a two-species Lotka-Volterra system with dispersal and competition that both species can coexist, if the species that is the worse competitor can outweigh this disadvantage by better dispersal and colonisation abilities. For certain heterogeneities in competition abilities (i.e., how efficiently a species can consume a resource locally) the dispersal advantage is not needed and both species can coexist in a source-sink dynamic.

Combining heterogeneity with niche theory (refer to Chapter 2) leads to a fundamental ecological hypothesis - the habitat heterogeneity hypothesis [25]. It states that diversity is larger in heterogeneous environments because [130]:

(a) the environment offers more possible niches for species to speciate on (evolutionary argument)

(b) the environment offers better chances of finding "sheltering" living conditions, e.g., a spot with a suitable temperature or protected nesting sites

More possible niches are related to a better exploitation of available resources in a location [131]. The historical origin of this hypothesis lies in the attempt to explain species diversity along the latitudinal gradient [25]. Analysing species above ground diversity from the poles to the equator shows a steady increase of diversity. A positive relationship between heterogeneity and animal diversity has been found in a meta-study [20], but the degree of the effect depends on the details of the studied system which where biased towards vertebrates [20]. Another problem arises, just like in the niche theory, in how to define heterogeneity in a given habitat. Depending on the species under consideration different aspects may be chosen as heterogeneous control variables. For animals, for example, a good environmental variable is the vegetation distribution, which of course cannot serve as an environmental variable when looking at plants.

The edge effect hypothesis is related to the habitat heterogeneity hypothesis. In principle, the effect of habitat heterogeneity is considered at a special location - the boundary of distinct habitat types. This hypothesis is more debated than the habitat heterogeneity hypothesis. Diversity and abundance can be quite different in ecotones compared to the adjacent regions. A large variety of edge responses were reported, for example higher abundance in butterflies [132] or smaller abundance of some tree species [133] or birds [134] at forest edge or higher diversity at ecotones in frogs and birds [135], see [136] for an extensive list of literature. Results depend on the taxa under study and the method used to define ecotones [137] which is often hard and ambiguous, just as in the definition of heterogeneity alone. Ries and Sisk developed a framework for edge effects [21] which builds on resource distributions, see Fig. 3.1 for illustration. The model considers species abundance responses at an ecotone between two (hypothetical) types of adjacent areas. They derive edge responses only from resource considerations. A habitat can hold a large amount (denoted as "high quality" habitat by the authors) or a smaller amount of resources (denoted as "low quality" habitat by the authors). Resources might refer to substances or services that one could find in a real habitat, e.g. nutrients, sunlight, nesting sites or pollinators that help species in their struggle for existence in a habitat. Adjacent resources can either be supplementary or complementary. Complementary means that resources on one side are not present on the other side, for example, in a forest-meadow ecotone grass is only present on the side of the meadow and trees (e.g., for nesting) are only present on the forest side. Supplementary resources serve the same purpose and can replace each other. To stick to the forest-meadow ecotone, for example the prey of wolves can contain rabbits living in the meadow as well as boars living in the forest, so each type

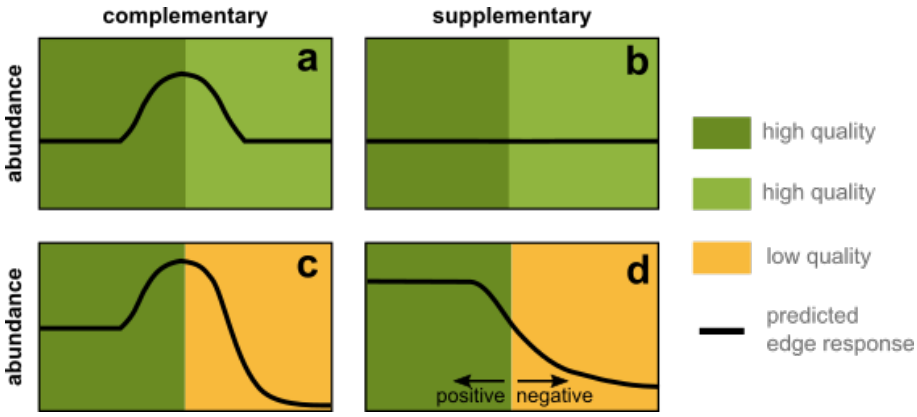

Fig. 3.1: Excerpt from the ecotone framework of Ries and Sisk [21]. The edge effect in abundance variance of species is derived from the underlying resource distribution, here depicted in greens and yellow. Resources are either complementary, i.e., species cannot find such resources on the other side of the ecotone , e.g., one side holds water and the other side fruits, or supplementary, i.e., they can be replaced by resources from the other side of the ecotone, e.g., two different kinds of fruit. If resources of similar quality are found in the habitats the edge response is either positive (**a**) for complementary or neutral (**b**) for supplementary resources. For low quality habitats adjacent to high quality habitats edge response can be positive if resources are complementary (**c**) or transitional for supplementary resources (**d**)). The transitional edge response can either be interpreted as a positive or a negative edge response depending on the direction.

habitat offers resources for the same requirement (foraging). For similar quality habitats, but supplementary resources a positive edge effect is predicted, see Fig. 3.1a, because species have access to both sides and can profit from finding different resources. Abundances at an ecotone of supplementary and qualitatively similar habitats will show no response to the edge, see Fig. 3.1b, because species find no different conditions at the edge. In case of qualitatively different resources the edge effect will be positive for complementary resources, but abundance will decrease the further a species gets into the low quality region because it needs access to the high quality habitat to stay alive. For supplementary resources the edge effect will be purely transitional and abundance will decrease with distance from the high

quality habitat. Depending on the direction this can be interpreted as a positive or negative edge effect.
The framework does not make any assumptions on the coupling strength between the habitats. Nevertheless, dispersal must be sufficiently high between areas for species to profit from complementary resources in adjacent areas. We will show with our model that this assumption is confirmed by *in silico* experiments in the next section. Overall the influence of dispersal on the diversity in meta-communities that live in heterogeneous environments is studied. Local and regional robustness will serve as a measure of diversity. We analyse the impact of edge effects and random heterogeneity in separate spatial scenarios. The main findings comprise a confirmation of the hump-shaped dispersal-diversity curve and a relation between edge effects and dispersal strength. Intermediate dispersal can lead to positive edge effects because of source-sink dynamics in a heterogeneous environment.
Based on the theoretical knowledge on how habitat heterogeneity and edge effects occur in model systems we gain hints on what scholars should look for in real systems. Fragmentation and destruction of species habitats are one of the major threats for ecosystems world wide. The consequences are more edges between humanly used areas and more natural areas as well as an effective decrease in dispersal rates as distances between suitable habitats grow. Our study thus serves as a valuable first step in the exploration on the effects of an increased number of edges on ecosystems.

3.2 Meta-Community Model

The local model (structure and dynamics) used in this chapter was originally proposed by Plitzko and Drossel to analyse the impact of different topologies of an otherwise homogeneous spatial network on the robustness of food webs [31]. We will now take the next step and explore the impact of resource heterogeneity. The model consists of several parts: The food web model, the spatial modelling and the modelling of the dynamics. The following sections explain the model in all details. For a compendious overview of the model refer to the spec sheet on page 40.

Food web model: Niche model

The food web model that generates the food web structures on the distinct patches is the niche model [26], refer to Fig. 3.2 for an illustration of the process described in the following paragraph. The niche model depends on two parameters: the number of species S and connectivity C. Species are characterised by an abstract trait n - the niche value - a random number in the interval $[0,1]$. Considering

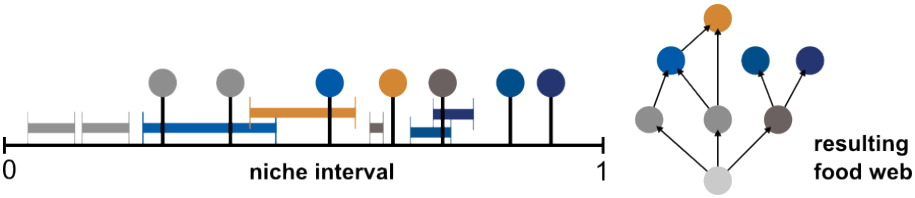

Fig. 3.2: Illustration of the construction of a niche model food web. Species are characterised by niche values (pins on the axis). Each species preys on a fraction of the niche axis (feeding ranges), indicated by coloured bars. Species whose feeding range does not cover another species are considered as basal and linked to the external resource (light grey).

metabolic theory, the niche value might be associated with a species' body size, see for example [30]. To determine feeding interactions each species is assigned a feeding interval r. The value of r is obtained by multiplying the niche value with a random value drawn from a beta-distribution of the form $P(x|1,\beta) = \beta \cdot (1-x)^{\beta-1}$ with $\beta = (1-2C)/2C$. Here C denotes the aforementioned connectivity. The choice of the distribution leads to $< r >= C$, so the feeding intervals will be in the size of the desired connectivity. The feeding center c positions the feeding interval on the niche axis. It is placed randomly between the niche value of the species and half of its feeding range, i.e., in the interval $[r/2, n]$. This allows the feeding center to be only smaller or equal to a species niche value, but lets the feeding range end at values potentially larger than the niche value.

All species whose niche values fall into the feeding interval of another species are considered as prey. With the placement of r it is possible for species to feed on species with a higher niche value, particularly the own niche value might fall into the own feeding range which would resemble cannibalism. Cannibalism is in our application omitted and self-links are removed from the network, although cannibalism occurs in nature, i.e., adult individuals preying on juvenile individuals in fish. Species that end up having no prey species in their feeding interval are considered as basal species. They are in turn linked to an external resource pool for calculating population dynamics.

In order to work with comparable food webs some restrictions are imposed on the food webs used in the simulations: All food webs have the same number of participating species S, have a connectivity in the interval $C \in [0.15 \pm 0.01]$, following empirical reasonable values [26, 31], and a fraction of basal species of one sixth of S, to control the energy input in the system [138]. All parameter choices are listed in table 3.1.

Tab. 3.1: Numerical parameter values that were used in the simulations that are presented here. Values are taken from [30, 31, 122].

Parameter	Symbol	Numerical value	Dimension
No. of species	S	18	
No. of habitats	Y	20	
Respiration rate	α	0.3	1/time
Competition rate	β	0.5	area/time
Ecological efficiency	λ	0.65	
Attack rate	a	6	area/time
Handling time	h	0.35	time
Allometric coeff.	x	4	
Size of resource pool	R_1, R_2	0.15, 3.00	mass/area
Initial biomass density	$B_i(t=0)$	$\in [0.001, 0.101]$	mass/area
Extinction threshold	B_{ext}	10^{-5}	mass/area

Spatial network and simulated scenarios

We use a spatial network of habitats that are in some way connected. Each habitat resembles a habitat where one instance of the food web resides. Heterogeneity is introduced by the distribution of resource on the spatial grid. The amount of resource a patch holds determines how much energy is available to the food web in this point of space. For simplicity only two types of habitats are distinguished: High and low resource habitats.
Two scenarios are analysed:

(1) A random arrangement of low and high resource patches with a fixed proportion of high and low resource patches

(2) A block-wise arrangement - one side of space holds a large amount of resource on each patch and the other side holds low resource on each patch.

Both scenarios are depicted in Fig. 3.3. Habitats are arranged in a one dimensional grid with periodic boundaries (closed chain of habitats). This means that all habitats have the same degree and we do not need to disentangle effects of heterogeneous degree distributions from effects coming from the resource heterogeneity. We will come to heterogeneous degree distributions in chapter 6 in the context of random geometric graphs.

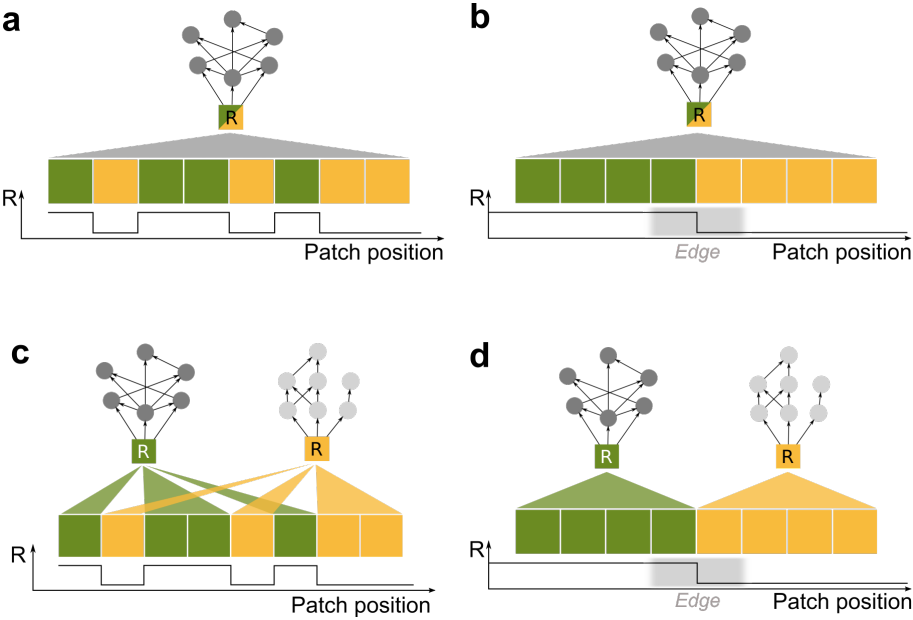

Fig. 3.3: Sketch of the four distinct simulation set-ups. Two spatial - a random resource distribution (**a**, **c**) and a block-wise resource distribution (**b**, **d**), and two trophic scenarios - the same food web on all habitats (**a**, **b**) or one food web type per patch type (**c**, **d**), are combined. The block-wise resource structure is suitable to study edge effects, whilst the random distribution aims at studying overall effects of heterogeneity.

On top of the spatial set up two different food web scenarios are placed:

(1) The same food web on all habitats: This models a homogeneous meta community and focuses on the resource changes in the spatial web.

(2) One food web per habitat type: This models two communities that live initially exclusive on their habitat type.

The second scenario is especially interesting for the edge region in the block-wise scenario, as it models two adjacent homogeneous communities that only interfere in the ecotone region. This results in four combinations of food web and space patterns that are displayed in Fig. 3.3.

Population dynamics

We use the bioenergetics approach proposed by Yodzis and Innes [139] to determine the biomass density B_i of a species i on a specific habitat u by equation (3.1)

$$\frac{dB_i^u}{dt} = \underbrace{\lambda \sum_{j \in \mathcal{G}_i} m_i^{-\frac{1}{4}} f_{ij} B_i}_{\text{ingestion}} - \underbrace{\sum_{k \in \mathcal{H}_i} m_k^{-\frac{1}{4}} f_{ki} B_k}_{\text{predation}} - \underbrace{\alpha m_i^{-\frac{1}{4}} B_i}_{\text{respiration}} - \underbrace{\beta m_i^{-\frac{1}{4}} B_i^2}_{\text{competition}} + \underbrace{B_i^{uv}}_{\text{dispersal}} . \tag{3.1}$$

The first term models a species' gain by ingesting biomass either from preying on other species or the external resource. The gain for species i preying on species j is modelled by a functional response f_{ij} that has the form of a Holling type-II [140]:

$$f_{ij} = \frac{a_{ij} B_j}{1 + a_{ij} h B_j}. \tag{3.2}$$

Here a_{ij} denotes the attack rate, i.e., the rate at which a predator i discovers prey j. The time for in- and digestion, cleaning and so on is summarised by the handling time h. Basal species only prey on one species, namely the external resource, but in principle predators can have more than one prey. Consequently, the predator needs to divide its time into hunting its various prey species that are summarised in the set $\mathcal{G}_i$. This means the attack rate is not the same for all prey species but could be for example proportional to the biomass densities of the prey species. For simplicity we assume in the following that the predator splits its time equally on all its prey species and replace a_{ij} by $\tilde{a}_i = a/|\mathcal{G}_i|$ the so called fractional foraging effort, with a fixed value for a for all species. This results in

$$f_{ij} = \frac{\tilde{a}_i B_j}{1 + \sum_{l \in \mathcal{G}_i} \tilde{a} h B_l} \tag{3.3}$$

for a single predator i -prey j interaction. The total ingestion gain for i is obtained by summing over all prey that are grouped in the set $\mathcal{G}_i$ and multiplying with the predators biomass density. Earlier models, for example Lotka-Volterra models, assumed a linear increase in per-capita ingestion rate for increasing prey or predator density [59]. This is not realistic for very large prey densities as each predator needs time to handle one catch of prey. The functional response should consequently saturate for large prey densities like the Holling type II functional response. Other forms for such a functional response are also possible, for example a Beddington-DeAngelis form [141, 142] that includes another handling time term accounting for wasted time by competing for the same prey item with another predator, but the Holling type II form is widely used and ecological plausible.

Only a fraction λ of ingested biomass is converted into biomass of the consumer, because of inedible or non-digestible parts. The parameter λ is called the assimilation efficiency. This efficiency is assumed to be the same for all species for simplicity, although different values, e.g., for herbivorous and carnivorous species have been proposed [139]. Numerical values used for all parameters can be found in Tab. 3.1.
The second term models the loss of species i being a prey itself to all predators in the set $\mathcal{H}_i$. The third term accounts for metabolic losses for the species that inevitably occur with respiration rate α. The fourth term is quadratic in the biomass density in i and models intraspecific competition with a rate β, for example, for mating partners or nesting sites or the spreading of diseases.
The last term models diffusive dispersal to the neighbouring patches of u that make up the set $\mathcal{N}_u$. The dispersal term is dependent on the parameter of interest in this study - the dispersal rate d

$$B_i^{uv} = d m_i^{-\frac{1}{4}} \sum_{v \in \mathcal{N}_u} \left(B_i^v - B_i^u \right). \tag{3.4}$$

Dispersal is modelled as diffusion, a fraction $d \cdot B_i^u$ of biomass is transferred to each of the neighbours. The relation between d and the respiration rate α determines the time scales between ecological and spatial processes.
All terms are scaled allometrically with the average body size of one individual of the species m_i, following the metabolic theory of biology [76, 77]: Biological rates scale with body size following power laws with exponents depending on the kind of rate. Respiration rate, for example, scales with $m^{-\frac{1}{4}}$ [77]. The scaling with body mass of all parameters is obtained by inserting the knowledge of such power laws in the rewriting of Equation (3.1) from individual numbers to biomasses, that is the number of individuals in a population divided by the average body mass of one individual, as demonstrated in [30]. It has been shown that allometric scaling enhances the stability of model food webs considerably [30,143]. Within our model the body size is derived from the niche value: We interpret the niche value n_i as the logarithm of the body size of a species

$$m_i = 10^{x \cdot n_i}. \tag{3.5}$$

The parameter $x > 0$ determines the interval between smallest ($n_i = 0$) and largest ($n_i = 1$) species and therefore the largest possible body mass ratio between predator and prey. Empirical values for predator-prey body mass ratios vary considerably [143], but the general trend is that most predators are larger than their prey.

We choose x to be 4 for all simulations shown in this section. This leads to predators that are around three times larger than their prey, considering the choice for connectance which determine the distribution of niche values on the niche axis. Species are considered extinct if their biomass densities fall below the extinction threshold of 10^{-5}, which is chosen in concert with the starting biomasses in the order of 10^2.

Spec sheet: Metacommunity Model

Food web model
Niche model: Species are characterised by niche value, feeding range, feeding center.

Dynamics
Bioenergetics approach: The evolution of biomass densities for a species encompasses gain and loss due to trophic interactions, respiration and competition losses and the dispersal term.

$$\begin{aligned}\dot{\mathbf{B}}_i^u =& \lambda \sum_{j \in \mathscr{G}_i} m_i^{-\frac{1}{4}} \frac{a f_{ij} B_j}{1 + \sum_{l \in \mathscr{G}_i} a f_{il} h B_l} B_i \\ &- \sum_{k \in \mathscr{H}_i} m_k^{-\frac{1}{4}} \frac{a f_{ki} B_i}{1 + \sum_{n \in \mathscr{H}_k} a f_{kn} h B_n} B_k \\ &- \alpha m_i^{-\frac{1}{4}} B_i - \beta m_i^{-\frac{1}{4}} B_i^2 + B_i^{uv}\end{aligned}$$

Spatial setting and dispersal
We arrange the habitats in a one dimensional grid with periodic boundary conditions (ring shape). A link between two patches enables diffusive dispersal for the species on these patches and the total biomass density change due to dispersal on a patch is determined by all its neighbouring patches $\mathscr{N}_u$.

$$B_i^{uv} = d m_i^{-\frac{1}{4}} \sum_{v \in \mathscr{N}_u} \left(B_i^v - B_i^u \right)$$

Heterogeneity
Heterogeneity is introduced by binary variation of energy influx between patches. Two settings are explored: Block-wise and random arrangement of distinctive habitats. Each setting comes in two variations - once with one food web on all habitats and once with two different food webs on the two types of habitat.

Scenarios and simulation procedure

For each scenario a simulation run consists of setting up the spatial topology and resource distribution, generating niche web(s) for the habitats and finally solving Equation (3.1) numerically. This results in time series of biomass densities of all species. A species whose biomass density falls below 10^{-5} is considered extinct and its biomass density is set to 0 during the rest of the simulation.

We are not interested in particular time series as we do not model real species and cannot interpret the time series in some sense. The goal is rather to understand general influences of heterogeneity on diversity and biomass densities across the trophic levels of a food web. This is accomplished by analysing mean values of ensembles of simulations. For one set of parameters one hundred simulations with starting biomass densities randomly chosen from [0.001, 0.101] are run. Each simulation consists of 20 habitats each starting with a food web of 18 species with 3 basal species. This was chosen because it is large enough for complex structure to emerge, but small enough to keep the computation time moderate.

The quantities we analyse are robustness, the fraction of surviving species, as a measure for diversity and biomass density. We will analyse overall and per trophic level robustness and biomass densities either per habitat (block-wise scenario) or as an average over all habitats (random habitat distribution).

3.3 Patterns in Heterogeneous Space and Ecological Time

Robustness and biomass

We begin the result section with a look at robustness for the different scenarios. Figure 3.4 shows regional robustness, i.e., robustness averaged over all habitats, as a function of dispersal strength for the random resource distribution scenarios in panels a (one local food web) and c (two local food web types). We focus on the scenario in panel a first. Robustness takes the form of a hump-shaped curve as a function of dispersal rate (black). Compared to an isolated system (grey dotted line), robustness is larger when dispersal is active. Robustness obtains a maximum for an intermediate value of the dispersal strength ($\log d = -3$). The robustness is plotted separately for the two types of habitats (yellow/green curves) in order to analyse the contribution of each habitat type. Robustness differs widely for the two patch types when dispersal is small. For increasing dispersal rate robustness in the low quality patches starts to converge to robustness of high quality patches. For large dispersal, when the overall hump is already falling, robustness is equal in both patch types as the patches become synchronised.

To distil the effect of heterogeneity we plot the result for a homogeneous system that holds exactly the same amount of resource (summed over all patches) as the

heterogeneous systems as the dashed curve. We observe that robustness in the homogeneous system is higher for large and small dispersal rates, but smaller in the region where robustness peaks in the heterogeneous system. The amplitude of the robustness increase is much larger when resources are heterogeneously distributed.

In the homogeneous system three mechanisms lead to an increase in robustness which is known from previous studies of homogeneous systems [31]. Those are: Rescue effect - species that go extinct only locally, due to fluctuations in starting biomasses, can recolonise a habitat from surrounding habitats, dynamic coexistence - dispersal opens more possibilities in phase space which might allow more species to coexist and the build-up of biomass reservoirs in part of the habitats - this might dampen fluctuations in biomass evolution and prevent extinction by large oscillations in biomass density. An inhomogeneous build-up of biomass is only possible when the system has some inhomogeneity itself. In the work of Plitzko and Drossel this was realised by a heterogeneous link distribution in combination with link-wise[5] dispersal [31]. This leads to biomass build-up in habitats with a large number of links. In our set-up the heterogeneity lies within the different amount of resource. The high quality habitats can serve as biomass sources for neighbouring low quality habitats as long as dispersal is not too large to lead to a synchronisation of patches.

Figure 3.5 illustrates this by showing biomass density as a function of dispersal, analogous to Fig. 3.4. The black curve shows regional biomass, exhibiting only little response to a variation in dispersal rate. Only the biomass for large dispersal rates decreases slightly. More interesting are the contributions from high and low quality habitats. For small dispersal the biomass flux from high quality patches is not sufficient to induce an increase in the low quality habitats. But from intermediate dispersal on biomass density increases in the low quality habitats as biomass is transferred from the high quality habitats, which serve as a biomass source. For even larger dispersal rates all habitats synchronise.

This “mass effect” is even more noticeable in the scenario with block-wise resource distribution (b). Figures 3.4b, d and 3.5b, d show robustness and biomass for this scenario, but this time evaluated for each habitat separately. For sufficiently large dispersal rates we see that robustness increases in low quality habitats adjacent to the high quality habitats (Fig. 3.4). Intensity and range of this effect increases with dispersal strength. Diversity even becomes higher in low quality patches than in high quality patches when dispersal is large enough. Biomass shows a similar

[5] Link-wise dispersal assumes that a fixed fraction of biomass is transferred through all links of a habitat into the neighbouring habitats. Another dispersal implementation would be patch-wise dispersal that assumes a fixed fraction of biomass leaves the habitat despite the number of links, which would lead to a smaller fraction of biomass per link in habitats that have more links.

trend, but decreases continuously into the low quality area (Fig. 3.5). The small amount of biomass that is transferred into the low quality area is, nevertheless, large enough to allow for the survival of species in these habitats that would not survive in an isolated habitat of this type.
Panels c and d of Fig. 3.4 and 3.5 show regional/local robustness/biomass density for scenarios with two different food webs, one per patch type. All observations stated above also hold for these scenarios and are even amplified in strength. Note that robustness can be larger than 1 in this scenario because the species pool of both food web types together is twice as large as the local species pool which serves as reference. The increase is especially striking when comparing Fig. 3.5 a and c: More biomass builds up in the scenario with two food webs and we observe a prominent hump in biomass over dispersal. This is because low quality habitats start to accumulate more biomass even for smaller dispersal rates as more species are present that can accumulate biomass. The synchronisation of low and high quality patches still happens at the same high dispersal rate, in accordance to the decrease in robustness in Fig 3.4 (c), indicating that less species survive.
The observed edge effects in robustness in the block-wise scenarios are also enhanced. We observe a large peak in robustness for intermediate dispersal strength, see Fig. 3.4d, in the low quality habitats adjacent to the high quality area. Species dispersing from high quality areas end up here and add up to species that are exclusively living in the low quality area. The influx from the high quality side is large enough to support viable populations in the ecotone region, especially larger than in the one food web scenario, when comparing Fig. 3.5b and d. Again this is due to more species that can accumulate biomass because of a larger species pool. For larger dispersal rates the mass effect reaches further into the low quality area and "assimilates" the habitats, i.e., species configuration starts to synchronise. Finally all habitats are identical when synchronisation is reached for large dispersal rates.
Variation in the respiration rate instead of resource distribution were analysed for the block-wise scenario for one food web on all habitats for variation [144]. The results were found to be analogue to the results stated here [144].

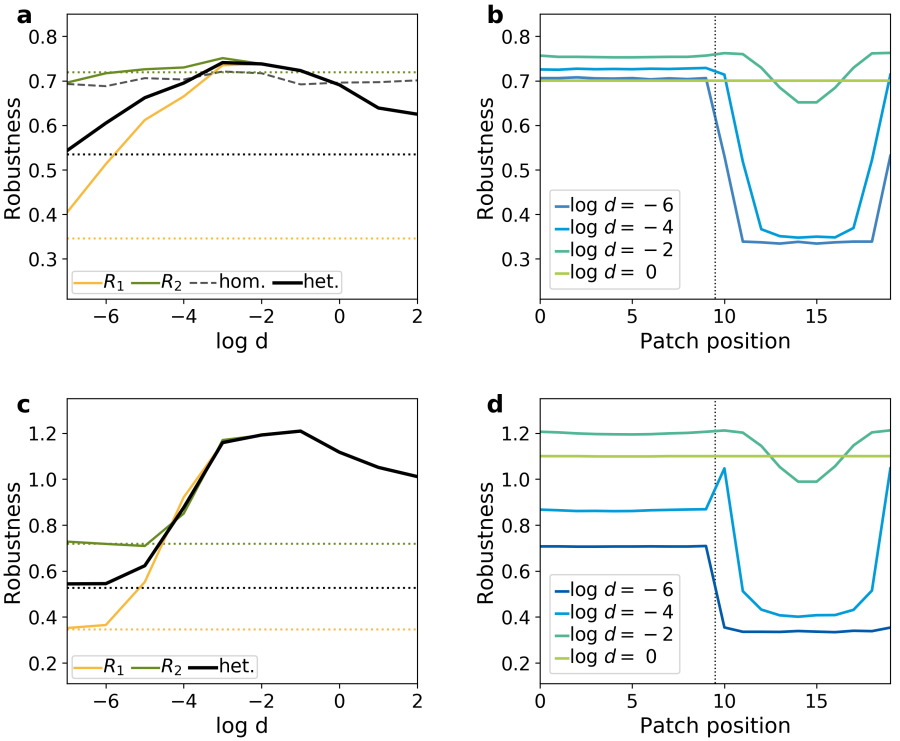

Fig. 3.4: Robustness for the different scenarios, labelling follows that in Fig 3.3. **a**: Regional robustness over dispersal rate (black). Yellow and green lines refer to the contributions of low and high quality patches, with the dotted baselines indicating their robustness values if in isolation. The dashed line refers to a homogeneous system with the same amount resource in total. **b**: Local robustness per patch for a block-wise scenario with the same food web on all habitats. The vertical line indicates the ecotone. **c**: Analogue to (a), but housing two different food webs on the two habitat types. **d**: Analogue to (b), but with distinct food webs on the distinct patch types. The ecotone is marked by the vertical line.

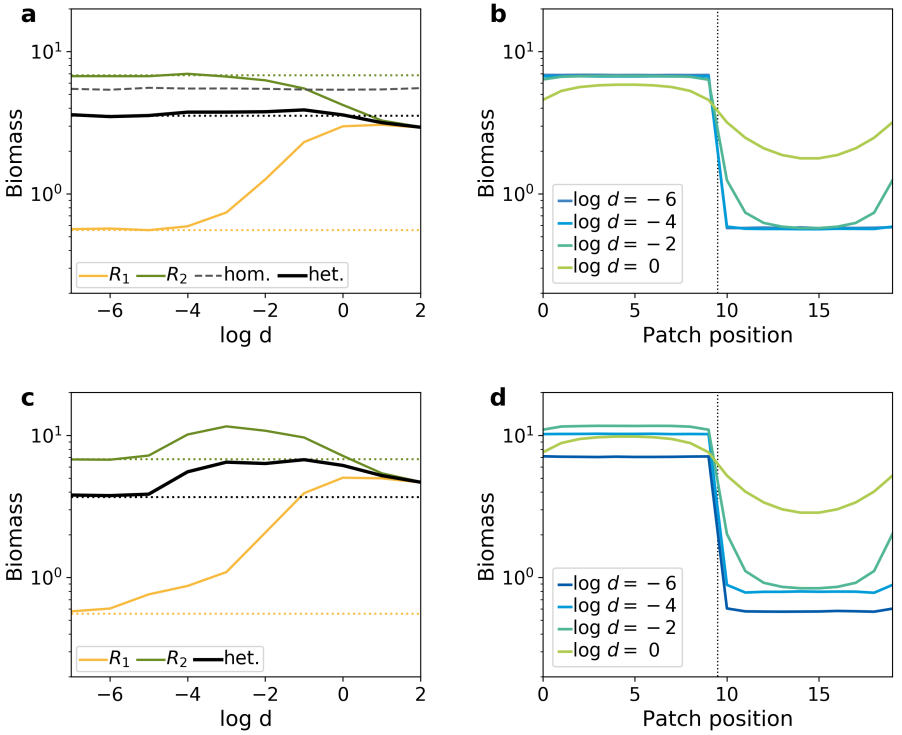

Fig. 3.5: Biomass for the different scenarios, labelling follows that in Fig 3.3. **a**: Regional biomass over dispersal rate. Yellow and green lines refer to the contributions of low and high quality patches, with the dotted baselines indicating their biomass values if in isolation. **b**: Local biomass for a blockwise scenario with the same food web on all habitats. The vertical line indicates the ecotone. **c**: Analogue to (a), but housing two different food webs on the two habitat types. **d**: Analogue to (b), but with distinct food webs on the distinct patch types. The ecotone is marked by the vertical line.

Trophic level structure

One key feature of food webs is the layered structure. We analysed robustness, see Fig 3.6, and biomass, see Fig. 3.7, separately per trophic layer to check if heterogeneity affects the layers differently. The robustness value is obtained by dividing the number of surviving species by the total number of species S that were initially on the habitat. This leads to a maximum robustness of $1/6$ for basal species as the fraction of basal species is restricted to $S/6$. We narrow our analysis to the scenarios with block-wise resource distribution to study hoe edge effects cascade through a trophic network.

Species on trophic layer 1 are the links between resource and food web as they directly gain their energy from the resource pool. *Per constructionem*, basal species comprise one sixth of the number of species in a food web. We observe that the basal layer is very robust in a system with one food web on all patches, see Fig. 3.6a. No basal species goes extinct in any patch for any dispersal strength. The resource distribution only affects the amount of biomass that builds up in the basal layer, see Fig. 3.7a. We observe larger biomass in high quality habitats than low quality habitats, just as expected. For two local food webs basal species of the two regions coexist in some parts of the spatial network, depending on the dispersal rate. This results in an increased robustness in the high quality habitats (small dispersal) or all habitats (large dispersal), see panel (d) in Fig. 3.6. For intermediate dispersal a peak in robustness appears in the low quality habitat adjacent to the high quality area as we have already seen in the full network. The biomass that builds up in the basal layer is smaller for the two food web scenario than for the one food web scenario, see Fig. 3.7d, but the shape of the curve is unchanged. The smaller values for biomass in trophic level 1 are a result of the behaviour of species on trophic level 2. Robustness and biomass for the second trophic level are shown in panels b, one food web, and e, two food webs, in Figs. 3.6 and 3.7, respectively. Trophic level 2 profits immensely from an enlarged species pool and builds up twice as much biomass in the two food web scenario compared to the one food web scenario. In high quality habitats species from both food webs can survive leading to a huge accumulation of biomass. This biomass in turn is dispersed into neighbouring habitats of low quality where we therefore also observe a robustness peak as in the full system. The large number of trophic level 2 species decreases the biomass in the first trophic level in the two food web scenario. This cannot be observed in the one food web scenario because the species pool is small and species rarely survive exclusively in low quality habitats and, thus, no large coexistence peak in the edge habitats can be observed.

Regarding the species on trophic level 3, we see that the low quality habitats only hold species that come in by dispersal from the high quality area in the scenario

with one food web. Further away from the border the robustness drops to 0 in the low quality area, the range depends on the dispersal strength. In the two food web scenario a small fraction of trophic level 3 species resides in the low quality habitats even in habitats far away from the border and for small dispersal rates. The reason lies in the better prey situation in this scenario: More species on trophic level 2 are present over the whole spatial network, so the nutrition situation for the higher level is improved. This leads again to a peak in robustness in the ecotone region.

The biomass distribution between trophic levels differs in the one and two food web scenarios. The former shows a steady decrease from basal to top level which is similar to a classical biomass pyramid. The two community system holds most biomass in the second trophic level. The third trophic level profits from that and gains the second largest amount of biomass while the basal layer suffers from large predator populations and thus has the smallest amount of biomass.

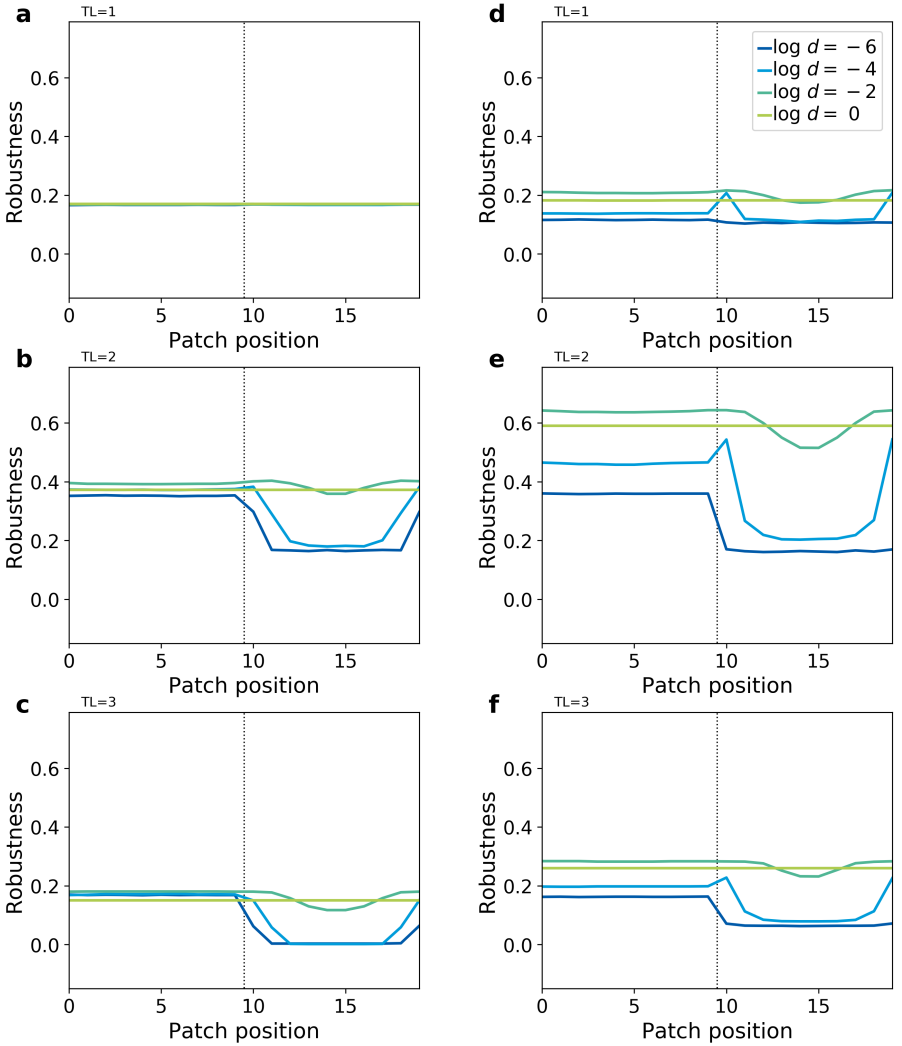

Fig. 3.6: (**a** - **c**): Local robustness per trophic level in a system with the same food web on all habitats and a block-wise resource distribution. (**d** - **f**): Local robustness per trophic level in a system with two different food webs on the different habitat types and a block-wise resource distribution. The ecotone is indicated by the vertical line.

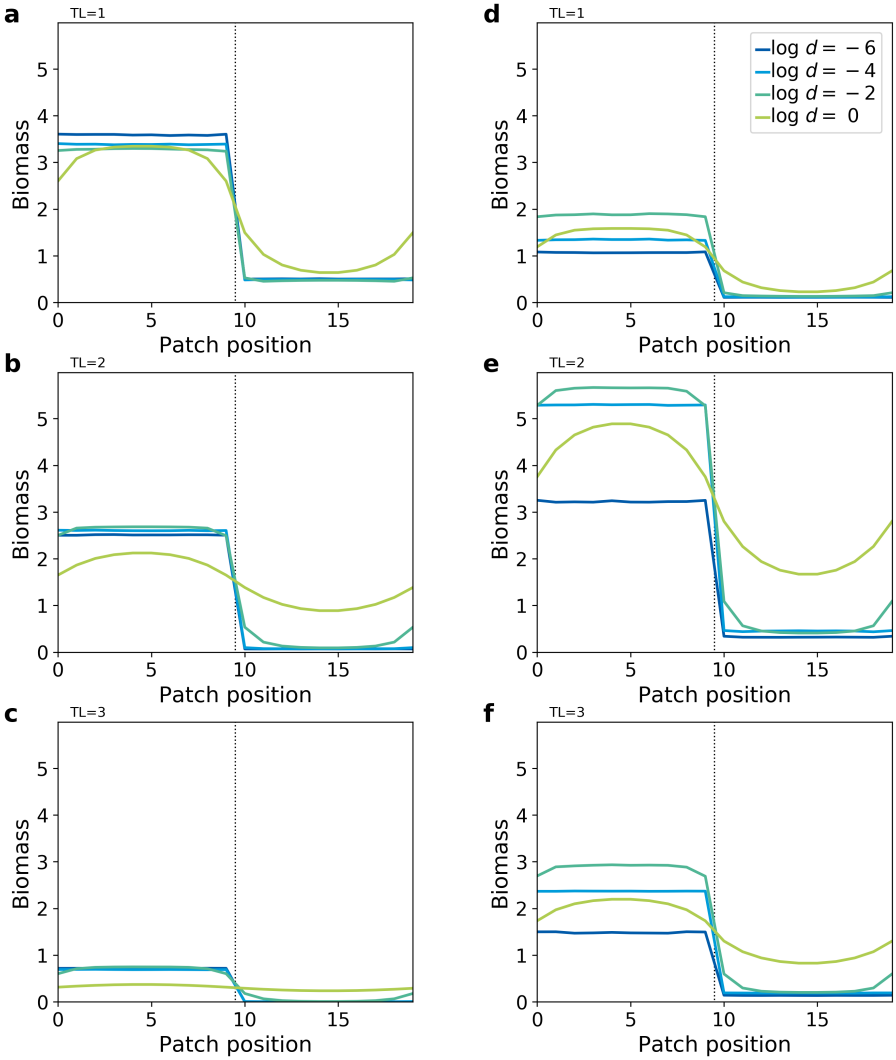

Fig. 3.7: (**a** - **c**): Local biomass per trophic level in a system with the same food web on all habitats and a block-wise resource distribution. (**d** - **f**): Local biomass per trophic level in a system with two different food webs on the different habitat types and a block-wise resource distribution. The ecotone is indicated by the vertical line.

3.4 Discussion

The results presented in this chapter show that diversity in large meta-communities with heterogeneous resource distribution is higher if dispersal is sufficiently large within an intermediate range. The reason is that the increased diversity is driven by source-sink dynamics: Biomass flows from high quality to low quality habitats. This only leads to coexistence and thus higher diversity for intermediate dispersal rates. Low quality habitats adjacent to high quality habitats can become the habitats with the highest diversity due to coexistence of species from both neighbouring communities, rendering them "biodiversity hot spots".

This work is the first to explicitly investigate meta-community behaviour at edges via computer simulations. Edges are located at the interface of high and low resource abundance. We observe different edge effects depending on dispersal strength, scenario and trophic level. All edge effects can be interpreted as source-sink effects. These results are compared to the edge response framework from Ries and Sisk [21] (hereinafter RS-model) that we introduced in section (3.1). Noteworthy, the RS-model refers to abundance of individual species, which we did not monitor. We only analysed biomass of the total trophic layer, so we will refer to trophic level or even the whole community as the unit of examination in the following. The edge responses that we observe in biomass can be classified as transitional, using the language of the RS-model, regardless of the scenario or dispersal rate, see Fig. 3.4 panels b and d. The RS-model predicts transitional edge response for a scenario in which the low quality habitat holds supplementary resources, i.e., resources that also exist on the high quality habitat. This is exactly what we set up in our systems as all basal species prey on a single resource which is present in all habitats and only differs in quantity. More interesting are the edge effects in diversity. With increasing dispersal rate the edge shows transitional positive up to neutral response, see Fig. 3.4 panels b and d. The dispersal rate leads to a specific edge response depending on the food web scenario. Positive edge response is observed in the two community system for even smaller dispersal rates due to the larger species pool. This observation holds for all trophic layers except for the trivial basal layer response in the one food web scenario where all habitats have the same configuration. This implies that the strength of dispersal plays a major role in the occurrence and amplitude of edge responses. The predictions of the RS-model do not take the strength of dispersal into account and base all predictions on resource distributions. Our results suggest that this can lead to biased results. For example, a positive edge effect could be expected for a trophic layer because of complementary resource distribution but a high dispersal rate would actually lead to neutral edge response. A more abstract and general version of the RS-model

discussed influences of ecological flows as dispersal [136] , but did not suggest how to include this in the predictive framework. Our model provides a theoretical tool to examine the influence of dispersal on edge responses. As our results show ecological flows must be taken into account to correctly predict edge responses, because the same resource configuration can lead to different edge responses for different dispersal rates. Our study thus represents a first step towards a predictive framework for edge responses on the metacommunity level.

Dispersal ability and behaviour is a trait in which real species differ vastly, for example in the size of home ranges [145] or maximum movement speed [146]. We modelled dispersal as a diffusive process. This is a solid first approximation, but when looking at real species a multitude of dispersal strategies is possible. Especially mammals show quite fascinating foraging strategies, both for hunting and avoiding predation like "sophisticated games of stealth and fear" [147]. Foraging theory talks of a "landscape of fear": Prey individuals might not use the whole area that would in principle provide food and shelter for them (suit their niche) to avoid meeting a predator [147]. This was also shown experimentally for monkeys in sub-Saharan Africa, that used part of their home range less in fear of leopards and baboons [148]. To model such a complex behaviour different models would be needed to address the different questions regarding ecotone diversity that arise in such a context.

The model we propose is well suited to be extended to further analyse issues around edge effects, for example regarding the depth of edge effects [149] or combined effects from multiple edges coming together [150]. For distance measurements of edge effects the model as it is presented here is too coarse grained. Edge effects, particularly the positive edge effects, only stretch over one habitat. For an in-depth measurement one needs to "zoom" into the habitats by rescaling biomasses and rates accordingly. The influence of multiple edges can be investigated by introducing more complex spatial structures, particularly two dimensional topologies like a square lattice with more complicated resource distributions [122]. The current resource distribution with only two types of habitats can be termed a "binary landscape contrast" referring to the terminology of [92]. This choice of landscape emphasises the joint effect of species interaction and dispersal [92]. An intermediate landscape contrast (e.g. gradient) is said to increase the influence of environmental filtering - communities are determined by the underlying environmental conditions [92]. This could be implemented within our model by introducing more habitat types, that gradually differ in their amount of resource. We expect for our systems that this results in the same edge responses between different habitat types, but with dampened amplitudes and no strict environmental filtering. Environmental filtering means that communities on habitats of the same type must be identical

which is not the case if edge effects due to source-sink dynamics occur because the neighbourhood of a habitat also determines the species composition.

Our result of a hump-shaped diversity-dispersal relationship for the scenarios with random resource distribution is in agreement with existing theory [31, 151, 152]. The heterogeneous system examined here shows a more slanted hump than a comparable (same amount of total resource) homogeneous system due to source-sink effects. High quality habitats serve as biomass sources for low quality habitat sinks. This cannot occur in homogeneous systems because biomass is evenly distributed among all habitats and the only effects that increase diversity are the rescue effect and dynamic coexistence. For an intermediate dispersal rate the heterogeneous system even supported more species than a homogeneous uncoupled system of habitats all holding large amounts of resource. Experiments also report similar results for this counter-intuitive result. In a community experiments with algae from the Baltic sea, Matthiesen et al. [153] prepared a spatial network of six patches of these algae communities. Dispersal between the habitats was simulated by moving small fractions of the biofilm between habitats. Heterogeneity was introduced by applying a six steps light gradient to the communities by gradual increased shading of habitats. A reference community obtained the full light intensity on all habitats. Diversity was larger in the heterogeneous systems even though less total energy was let into the meta-communities. This complies with our result and emphasises that the total amount of resource is not the most important factor determining species diversity, but the interplay of resource distribution and dispersal.

There are always two sides of a coin. Our results support the habitat heterogeneity hypothesis: More species can coexist in a heterogeneous environment compared to a homogeneous system for sufficient dispersal rates. This effect vanishes as soon as the dispersal rate is too high or too low and the heterogeneous system hosts less species because resources on high quality habitats can either not be used in other habitats (low dispersal) or swamp the system and cause synchronisation (large dispersal). Low dispersal in real meta-communities might be triggered by habitat destruction that leads to longer ways for species between intact habitats and in turn to smaller dispersal rates. This might lead to less diversity in those systems and emphasises the integrity of living environments. Another implication is that landscapes must be considered on a larger scale. Not only high quality habitats, but also their surrounding should be examined when, for example, making conservation management decisions. Landscape ecology as a relatively young subdiscipline of ecology [154] should be more intertwined with community ecology because ecological processes occur on all spatial and temporal scales.

3.5 Conclusion

We showed that heterogeneity can enhance diversity if dispersal has a sufficient strength. The same intermediate dispersal rate can also lead to positive edge responses. The reason is a source-sink process that transfers biomass from habitats with much resource to regions with less resource and thus enables species to survive in habitats by a steady influx of biomass from outside. The habitat heterogeneity hypothesis is insofar confirmed in the context of meta food webs, but with restrictions to intermediate dispersal rates. Heterogeneity is not *per se* beneficial for species diversity. For a correct prediction of species diversity at ecotones coupling strength between the two biomes need to be taken into account.

4 A New Evolutionary Food Web Model: Merging Body Mass and Webworld

Nothing in biology makes sense except in the light of evolution.

Theodosius Dobhansky

To study ecological patterns on large spatial and temporal scales it is necessary to incorporate speciation into a model [155] to account for the emergence of new species through evolution. There are several options to implement this in a model. One possibility is to create a *species pool* either before a simulation or on the fly and insert single species of this pool one after another into the system under study [156]. This implements the basic idea that is behind island biogeography [56]. There, islands see a steady influx from species coming from the mainland. The strength of the flux depends on the distance between mainland and island. How species arise on the mainland is left open (and is of no relevance to the islands) and the entirety of species on the mainland resembles the said species pool.
Another option is to let existing species evolve locally according to some set of rules and include those species in the next time step. This is the option that is usually incorporated in evolutionary food web models, because one is interested in studying the trophic network structure over time and seeing how the network evolves as a whole. The network structure is re-evaluated after the emergence of a new species that alters the network structure. The way of calculating who dies and who lives is often modelled by population dynamics, for which we saw an example in chapter 3. This is not feasible for a large number of habitats and species due to computational constrains.
This chapter introduces a new body mass structured evolutionary food web model, developed during this thesis, that relinquishes population dynamics in favour of a self-consistent equation to calculate long term biomass densities of species. First, existing theory on evolutionary food web models will be reviewed and the Webworld model [27] will be explained in detail as it served as a blue print for the new model. We will then give some impressions on the resulting dynamics and

structures and briefly show that those are robust to parameter value changes. The next chapter will then show the power of the new model to be used as a tool in studying macroecological patterns.
The model introduced here is presented in the article *The concerted emergence of well-known spatial and temporal ecological patterns in an evolutionary foodweb model in space* co-authored by Barbara Drossel which is submitted to Scientific Reports [157].

4.1 Evolutionary Food Web Models

Food web models try to capture the characteristic properties of food webs to give the researcher a generator for structures that approximate food webs. Evolutionary food web models try to find simple rules that govern species turn over. This means that food webs keep their overall structure, but the elements composing the food web (the species) change over time. The term "evolutionary" does not relate to the biological evolutionary process that drives speciation. Speciation is a complex entanglement of processes on genetic, individual and population level, see section 2.2. Evolutionary food web models do not make any assumptions on such detailed processes. They just assume there is speciation, arbitrarily creating diversity, without detailing how this speciation process works. Concrete implementations of the speciation dynamics is then up to the model and will normally be some simple rule on how existing species are varied to create diversity. A necessary property for such a model is a definition of what a species is, namely what traits define a species. Species diversity is actually trait diversity in such a model.
One of the first evolutionary food web models in the literature was the Webworld model [27]. The Webworld model defines species by a trait vector. Traits have no clear biological meaning but are chosen from a random matrix. Speciation is implemented in varying entries in the trait vectors thus creating diversity. We will explain the Webworld model in more detail in the following section 4.2.
Another approach, which is in a way a contrary idea, is to model species only by one trait - body size or body mass - a so called master trait [158, 159]. It is based on the observation that species normally feed on smaller species which makes food webs often body size structured. Furthermore, nearly all biological rates scale allometrically with body size (metabolic theory [77]) as well as other functions like locomotion [146], so picking body size as a master trait captures a lot of biology with the smallest number of parameters.
An example is the model of Loeuille and Loreau that chooses body size as the only trait in an evolutionary food web model [160]. Species feed on other species if their body size falls into the feeding range of the other species, similar to the niche

model [26]. Feeding range and feeding center are global parameters in this model. Population dynamics determine which species survive. New species enter the network by varying the body mass of species present in the network. This model yields body mass structured food webs with continuous species turn over, but the structure is nearly static. Allhoff and Drossel analysed this model further and came to the conclusion that feeding range and feeding centre need to be variable in some reasonable ranges to get more dynamic food web structures [161]. A spatial extension of a small number of coupled habitats of this model was analysed in [162] and found that species composition mainly depends on dispersal strength. Allhoff et al. developed a new model that includes varying body mass, feeding range and feeding centre [28]. The drawback with this model is that population dynamics are slow. After each speciation event the biomass densities of all species are numerically calculated which is a very computationally demanding step. This means that this model can only be used in small metacommunities with about four patches, like in [163]. We need another model for the analysis of macroecological patterns. An alternative approach is to replace population dynamics by a more abstract calculation of which species survives. Rogge et al. proposed the "survival index" for this calculation [29]. Still, species are characterised by body mass, feeding center and range. The survival index is inspired by population dynamics and takes into account the number of prey and predator per species as well as the trophic level and a competition function. In the end each species is assigned a number and if it is larger than 1 a species survives. This is computational fast, but biologically "fuzzy".

The evolutionary food web model we present here sticks to the idea of replacing the population dynamics. It keeps body mass as the master trait but replaces the survival index by the self-consistent population equation from the Webworld model. The following paragraph will describe the Webworld model in detail to make clear which ideas were borrowed from it and which were not when turning to the explanation of the new model in section 4.3. For a quick review and comparison between the Webworld and the new model refer to the spec sheets on page 64 and 65.

4.2 Webworld Model

The Webworld model [27] was introduced in 1998 to study questions like: "Does evolution stop at some point or is it continuous?". It was one, if not the first, model to incorporate evolutionary dynamics into a fully-fledged food web framework. The evolutionary process in Webworld acts on species which are characterised by an abstract trait vector with length L. A speciation event takes a species, copies it

and randomly changes one of its features, i.e., an entry in the trait vector is changed into another feature from a global feature pool. The original species is unaltered and also stays in the system. This feature pool mimics a pool of biological traits, like for example claws, shell, night sight and similar. The network structure emerges by introducing a random "score matrix" that dictates how a feature scores against another feature and has a fixed size $K \gg L$. The score matrix with entries m_{ij} is chosen such that the first half (entries with $i < j$) are taken from a Gaussian distribution around zero with a variance of 1 and the second half of the entries is just the negative of the first ($m_{ij} = -m_{ji}$). This makes sure that each pair of features brings advantages for one side and disadvantages for the other. Combining the species definition (trait vector) and the score matrix allows to calculate the effect of one species on another. A species having a positive score in a relation to another species is interpreted as a gain for this species, a negative would imply a loss of one species interacting with the other. Negative scores are not taken into account and are instead set to zero. The definition of the score between species n and n' is given by

$$S_{n,n'} = \max\left\{0, \frac{1}{L}\sum_{i\in n}\sum_{j\in n'} m_{ij}\right\}. \tag{4.1}$$

To ensure that the scores have a root mean square value close to one, scores are divided by the length of the trait vector L.
Who eats whom is determined by the scores. The strength of links is not only determined by the scores, but also by competition. The idea behind is that species with the same set of prey might interfere with each other, e.g., by hunting the same prey item and only one individual can finally consume it which results in wasted time for the competitor. The competition rule in Webworld is straightforward. The best predator of each prey, i.e., the species with the highest score S_n^M, is the reference scale for all other predators of this particular prey n. The available prey is shared among all predators following the rule

$$F_{n',n} = \max\left\{0, 1 - \frac{S_n^M - S_{n',n}}{\delta}\right\} \tag{4.2}$$

with $F_{n',n}$ being the fraction of the available prey n that the predator n' obtains (before normalising). The parameter δ can be tuned to strengthen (smaller δ) or weaken (larger δ) competition. Normalising the $F_{n',n}$ gives the final link strengths in the food web and the actual shares of the predators on each prey

$$\gamma_{n',n} = \frac{F_{n',n}}{\sum_m F_{m,n}}. \tag{4.3}$$

One species, the external resource or species 0, builds the basis of the food web and has a trait set that does not change. The resource has a fixed size of $R = \lambda N(0)$. Any species feeding on this special species has an entry $\gamma_{n,0}$ in the interaction matrix and gains a fraction of $\gamma_{n,0} \cdot R$ by preying on the resource. Gains of species n preying on other species are summed over all prey species n'. The overall gain is the sum of all gains

$$N_{\text{gain}}(n, t+1) = \gamma_{n,0} \lambda N(0) + \sum_{n'} \gamma_{n,n'} \lambda N(n', t) \tag{4.4}$$

with biomasses $N(n')$. Predation on the one side causes losses on the other side (prey side). Webworld assumes that a fraction λ of each prey population can be distributed among the predators. This is noted in the diagonal entries $\gamma_{n,n}$: if n is a prey species there will be an entry of -1, in all other cases and entry of 0.
Bringing all these pieces together in one equation [27] that determines the population sizes N Webworld defines

$$N(n, t+1) = \gamma_{n,0} \lambda N(0) + \sum_{n'} \gamma_{n,n'} \lambda N(n', t) + \gamma_{n,n} \lambda N(n, t). \tag{4.5}$$

Repeated iteration of equation (4.5) gives stationary values for all populations [27]. This population values are interpreted as the mean population sizes after several generations. It is not to be confused with an explicit population dynamics equation as used in chapter 3. This model works on evolutionary time scales and completely abstracts from faster dynamics like predator-prey dynamics. Still, the only information that is included is the network structure, which is assumed to be constant over some time. The evolutionary process alters the network structure and so the population sizes change over time. A species that has a population size N below 1 is considered extinct. This extinction threshold N_{ext} is chosen arbitrarily. Together with the fraction of resource that is transferred into the network R it determines the number of species that can at most exist in a network $S_{\max} = \frac{R}{N_{\text{ext}}}$. The evolutionary dynamics of the Webworld model result in complex trophic networks that undergo species turn over until a “frozen state” is reached, where no new species can stay in the system [164]. This can be regarded as an unrealistic feature as real ecosystems show a recurrent creation of new species and no frozen configuration. Species number and number of trophic levels can be determined by the parameter choice of R, λ and δ. A larger λ increases the biomass that is transferred to higher levels and thus leads to more trophic layers in the resulting networks. Larger δ leads to less species with larger populations within a trophic layer, in the extreme case the food web will turn into a food chain.

An estimation of the maximum height of the resulting food webs can be made, when assuming such a simple food chain, instead of a complex food web, i.e., only one species per trophic level. In that case equation (4.5) simplifies to

$$N_i = \lambda N_{i-1} - \lambda N_i, \tag{4.6}$$

the index refer to trophic level. Expressing the population of one trophic level in terms of the lower trophic level

$$N_i = \frac{\lambda}{1+\lambda} N_{i-1} \tag{4.7}$$

and plugging in the definition of the external resource pool $N_0 = \frac{R}{\lambda}$ leads to the overall equation for the population size on trophic level i (besides the top level that has no loss term)

$$N_i = \frac{\lambda^{i-1}}{(1+\lambda)^i} R. \tag{4.8}$$

The maximum chain length can be determined by calculating i for a given extinction threshold $N_i > N_{\text{ext}}$ using the population size of the top level that is $N_{\text{top}} = \frac{N_i}{\lambda}$

$$i < 1 + \frac{\log\left(\frac{N_{\text{ext}}}{R}\right)}{\log\left(\frac{\lambda}{1+\lambda}\right)}. \tag{4.9}$$

For the extinction threshold of $N_{\text{ext}} = 1$ and the later used values of $\lambda = 0.65$ and $R = 25$ this would give a maximum trophic level of 4. For real network structures the realised trophic level will be rather less than this value obtained for a chain because not all species in lower trophic levels will necessarily have a predator.
The Webworld model underwent a lot of modifications and extensions. Drossel et al. included a more realistic functional response term that allowed for a constant species turn-over [164]. Recently, the Webworld model was analysed in a small metacommunity framework (25 habitats) and appeared to give robust results to a plenitude of perturbations, e.g., stochastic dispersal between patches [165]. All references in the next section that are Webworld related refer to the original version that was introduced above.

4.3 Modified Model

The new model combines body mass as a master trait with competition and population equations from the Webworld model. In more concrete terms, the scores

from the Webworld model are replaced by attack rates, that are derived from body mass scaled feeding kernels, as used for example in [28, 29].
Species are now characterised by their body mass m, a feeding center f and a feeding range s just like in the niche model [26]. Due to the large differences in empirical predator and prey body masses [166] we measure all body masses logarithmically scaled. A species is prey of another species if its body mass lies inside the feeding interval of the predator. The feeding interval of a species is determined by an allometric feeding kernel, i.e., a Gaussian with a cut-off of one feeding range around the feeding center. The raw strength of a feeding interaction between predator i and prey j is then given by

$$a_{ij} = e^{-\frac{(f_i - m_j)^2}{2s_i}} \theta\left(\frac{|f_i - m_j|}{s_i}\right) \tag{4.10}$$

with the Heavyside-function θ that cuts links lying outside of an interval of one feeding range around the feeding center to omit that every species is connected to every other species. The next step is, like in the Webworld model, including competition between all predators of one prey species. We keep the same idea of comparing all predators with the best predator. This is the predator k with the largest attack rate $a_j^{\max} = \max(a_{ij})$ for a fixed prey j determined from the feeding kernel in this approach. Instead of (4.2) we use a slightly modified version with $\Delta a_i = a_j^{\max} - a_{ij}$

$$F_{ij} = \exp\left(-\left(\frac{\Delta a_i}{\delta}\right)^2\right). \tag{4.11}$$

The reason is that the linear competition is too insensitive for small differences between predator attack rates in a one dimensional trait space as the one used here. Smoothing out the competition function leads to less strong competition for species close to having the best attack rate and also lets species that are further away from the best attack rate gain some share of the prey. The idea is still the same as in Webworld.
The following procedure of determining the actual population sizes is then completely analogue to the Webworld dynamics. We use equation (4.5) to determine the long term average population sizes, using the new defined values for F_{ij}, to determine the non-diagonal elements of γ.
The meaning of the three parameters R, λ and δ stays exactly the same. The external resource or specie 0 is here defined by an immutable species with body mass $m_0 = 0$ and a size of R.

Tab. 4.1: Overview of model parameters with corresponding values used in simulations, if not stated otherwise. We will refer to these values as standard parameters in this thesis.

Parameter	Symbol	Numerical values
Efficiency	λ	0.65
Competition strength	δ	0.25
Resource per habitat	R	25
Speciation width	q	2
Feeding center interval	$f_{\min}, f_{\max}$	3, 1
Feeding range interval	$s_{\min}, s_{\max}$	0.5, 1

Speciation

New species are derived from existing species by slightly changing the existing trait set. The speciation rules follow those used in the model of Rogge et al. [29]. First, body mass (remember all body mass values are scaled logarithmically) of the new species m_{new} is taken from an interval, defined by the parameter q, around the body mass m_{old} of the existing species $m_{\text{new}} \in \left[q^{-1}m_{\text{old}}, qm_{\text{old}}\right]$. Second, the feeding center f is chosen from an interval below the new species' body mass defined by two parameters $f_{\min}$ and $f_{\max}$ following $f \in [m_{\text{new}} - f_{\min},\ m_{\text{new}} - f_{\max}]$. Finally, the feeding range is random-uniformly chosen from the interval $[s_{\min}, s_{\max}]$ determined by another pair of parameters $s_{\min}$ and $s_{\min}$. Any newly created species is added to the existing food web and equation (4.5) is used to determine the biomass densities of all species. A species with a biomass density below 1 is considered extinct and removed from the network.

The values that we use for the speciation parameters are summarised in Table 4.1. The choice of the speciation parameters determine the final shape of the food webs in several ways. A wider (smaller) interval for new body masses allows to faster (slower) reach body mass ranges that are far away from existing species. In combination with the intervals for feeding center f and feeding range s this determines how far apart trophic levels lie. We choose that the feeding interval must lie below a species' own body mass to omit loops in the networks. This resembles the trend in empirical data that predators are larger than their prey [166]. Nevertheless, food web structure is quite robust against changes in the numerical values for the parameters, as we will illustrate in the next section.

Simulation procedure

Prior to running the dynamics, a starting species is created that feeds on the resource. This species serves as the seed for the evolutionary dynamics. In subsequent simulation steps, a species is chosen randomly (weighted by biomass densities) and a speciation event is performed with this species as a blue print. The biomass densities are evaluated each time with the new species under consideration. If the biomass of a species is smaller than the extinction threshold of 1 the species is removed from the network and the populations are calculated again until no further extinction events happen. Step by step a network structure emerges. The simulation is run for a fixed number of steps (speciation events), in this chapter 10^6.

Spec sheet: Webworld Model

Species
Characterised by a trait vector with L random traits from a trait pool. Traits model features (behaviour or morphology), e.g., thick shell or night sight that give species (dis)advantages in interactions with each other. Basis of a network is a species with an immutable trait set and biomass R.

Interaction
Traits "score" against each other. Weight and Sign of the score are given by a random score matrix. The total score of a species against another is the sum of all scores from all trait combinations. If this results in a negative value the score of this interaction is set to 0.

Competition
Scores are modified by comparing each score to best achieved score (regarding one prey n)

$$F_{n',n} = \max\left\{0, 1 - \frac{S_n^M - S_{n',n}}{\delta}\right\}.$$

Normalisation $\gamma_{n',n} = F_{n',n} / \sum_m F_{m,n}$ gives the final interaction strength under consideration of all predators m of a prey n for the interaction of the predator-prey pair n' and n.

Population sizes
Basal species feed on external resource, modelled via $R = \lambda N(0)$, all other interactions are scaled with efficiency λ. Populations are determined by

$$B(i) = \gamma_{i,0} R + \lambda \left(\sum_j \gamma_{ij} B(j) - \gamma_{ii} B(i) \right) \quad \text{with} \, \gamma_{ii} = \begin{cases} -1, & \text{if i is prey} \\ 0, & \text{otherwise.} \end{cases}$$

Extinction occurs for species with B(i) < 1.

Speciation
A new species inherits all traits but one from an old species. The deviant trait is randomly chosen from the trait pool. This mimics random mutation.

Spec sheet: Modified Model

Species
Species are only characterised by body mass m, feeding center f and feeding range s. Basis of the network is an immutable species with body mass 0 and biomass R.

Interaction
Gaussian feeding kernel determines attack rate between predator i and prey j

$$a_{ij} = e^{-\frac{(f_i - m_j)^2}{2s_i}} \theta \left(\frac{|f_i - m_j|}{s_i} \right). \tag{4.12}$$

Competition
Comparing attack rates with that of the best predator (regarding one prey species j)

$$F_{ij} = \exp\left(-\left(\frac{\Delta a_i}{\delta} \right)^2 \right).$$

Normalisation $\gamma_{n',n} = F_{n',n} / \sum_m F_{m,n}$ gives the final interaction strength under consideration of all predators m of a prey n for the interaction of the predator-prey pair n' and n.

Biomass densities
Same equation as in Webworld, but with modified values for interactions γ

$$B(i) = \gamma_{i,0} R + \lambda \left(\sum_j \gamma_{ij} B(j) - \gamma_{ii} B(i) \right) \quad \text{with} \gamma_{ii} = \begin{cases} -1, & \text{if i is prey} \\ 0, & \text{otherwise.} \end{cases}$$

The extinction threshold is set to B(i) < 1, so species with smaller biomasses are removed from the network.

Speciation
A new species is created by copying the body mass of an old species, varying it in some interval and assigning feeding center and feeding range according to the new body mass.

4.4 Resulting Structures and Their Robustness

Figure 4.1a shows an exemplary time series for the dynamics that emerges in the new model. The parameters can be found in Table 4.1. Parameters are chosen in a way that the resulting network structure is complex, but not too large, so that we can use it on a large amount of habitats in the next chapter. The left axis denotes logarithmically scaled body mass as we plot the body masses of all species at each point in time. The right (blue) axis monitors the overall number of species in the habitat over time. The number of species shows only small fluctuations around the average number of 22 species. At most 25 species can persist in this network, because of the choice of $R = 25$ and an extinction threshold of 1. The time series already indicates that lifetimes of species differ widely, as we can observe a large variety in the length of body mass lines. Long, continuous lines indicate long lifetimes and small lines/dots indicate short times of presence of a species. There happen no large extinction avalanches that eradicate large fractions of species at once. Another positive aspect is that the dynamics does not run into a frozen configuration that prevents the establishment of new species. This was reported for other models [29,160] and can be fixed by including a small random extinction rate [29]. The model proposed here does not need any kind of external extinction rate, but produces a constant species turn over.

Concrete food webs and their rank abundance curves for three explicit points of the time series (dashed vertical lines) are shown in Figure 4.1b and c. Food webs show the characteristic layered structure with a decreasing number of species from lower to higher trophic levels. The number of species per trophic level is due to the choice of parameters and can be tuned to some extend by variation of λ and R, see section 4.4. Rank abundance curves as one form of displaying the SAD of the food webs show the empirically expected shape of a small number of species having large abundances and many species having small abundances (most species are rarely observed [14]). Compared to empirical data the ratio between largest and smallest abundances is small. In the shown examples the food web that shows the largest range of abundances has a maximum abundance that is only 1.78 times the smallest abundance. Natural systems show differences that are several magnitudes larger [6, 167]. As the new model is only one dimensional and natural systems are normally assumed to have a high-dimensional niche-space we expect that the difference in abundances would be more distinct in a higher dimensional model. Another aspect is the similarity of the basal species. As we can see in the network pictures and time series basal species are very similar in their traits, some are even identical when comparing predator sets. If one groups those species together into trophic species this alters the SAD as it reduces the number of basal species and

assigns larger abundances to the grouped species. Without grouping for trophic species the SADs of the networks show that the rank of a species is slightly correlated with trophic level. Basal species crowd the higher ranks, meaning lower abundances. They are numerous and thus suffer most from competition. Species with a higher trophic level have less competitors and a large set of prey and can thus build up higher biomass densities. Additionally we chose a quite high value for λ which transfers more than half of the energy build in one trophic level to the next level, which also strains the basal layer.

Brief Parameter Study

The model has the advantage of relying only on a handful of parameters. Nevertheless, emerging structures should not depend on a specific set of special parameter values, but be robust against (small) changes in the concrete values. We will therefore demonstrate that the particular choice of parameter values in a reasonable regime does not alter the observed network structure too drastically. Each parameter influences the emerging food web structures in a way that we will briefly display here. We split this section into two subsection, one regarding the original Webworld parameters and one regarding the speciation parameters.

Food Web Parameters

We review the influence of the original Webworld parameters: Resource input, ecological efficiency and competition modulation to build up intuition for the model.

Resource input and efficiency

The resource input R limits the available energy in the system. In combination with the extinction threshold it limits the number of species. We choose the extinction threshold to be 1, thus R species can at most reside in a network. We therefore expect larger networks with increasing R, both in terms of species number and height of the food web (maximum number of trophic levels).
Figure 4.2 displays example time series and food webs for increasing values of R and confirms the assertions we made. With increasing resource input more species on more trophic levels appear. The food webs show that the basal levels are more crowded than top levels which reflects the donor control principle that Equation (4.5) implements. The exact distribution of species (and biomasses) between the trophic layers depends of course on the value of the efficiency λ that determines the fraction of energy that is transferred from one level to the next.

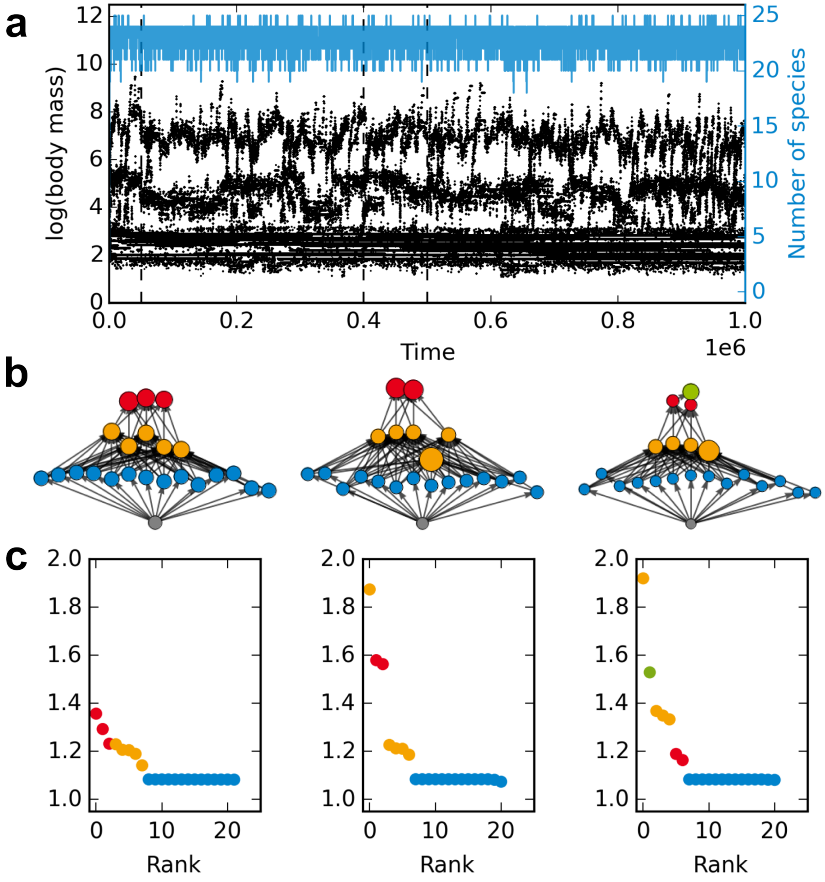

Fig. 4.1: **a**: Example time series for one habitat. We plot body masses of all species present at a point in time as well as species number (blue curve) over time. **b**: Example food webs from three points in the time series of marked as dashed lines ($t_1 = 5 \cdot 10^4$, $t_2 = 4 \cdot 10^5$ and $t_3 = 5 \cdot 10^5$. Food webs have a layered structure. Colour refers to trophic level (blue: TL = 1, yellow: TL = 2, red: TL = 3, green: TL = 4). **c**: Species abundance distributions in a rank abundance plot for the networks. Most basal species are not abundant and have thus high ranks.

Figure 4.3 shows the number of species per trophic level for increasing resource input for two different efficiencies (panel a small efficiency $\lambda = 0.1$, panel b larger efficiency $\lambda = 0.65$). The height of the food webs (maximum trophic level) is smaller for a small efficiency as less energy is transported into higher levels. The value of efficiency determines how fast species number decreases from one trophic level to the next. Note that species number is displayed logarithmically, the roughly linear decrease of species number with trophic level indicating the exponential decay which can be expected by only giving the same fraction of biomass into each higher level. Larger resources lead to more species in each trophic level, shifting the curve along the y-axis.

Figure 4.4 shows example time series for increasing values of efficiency for the standard value for $R = 25$. The standard value of $\lambda = 0.65$ lies between the two larger efficiencies shown. For small values all species have small body masses and only crowd the lowest trophic positions as the energy loss across two levels is too high to support species further up in the network. With increasing efficiency the number of levels increases and for large efficiencies networks with five stable trophic layers build up.

This means that R and λ together determine the network size and the ratio of species between trophic layers. This provides a neat tool to produce food webs with certain specifics, in this case species pyramids. It has to be noted that this model cannot produce inverse biomass pyramids, as for example common in aquatic food webs, because efficiency cannot exceed 1.

In foresight of the larger systems we want to analyse in the next chapter, we choose a rather small value of R and a high value of λ for the standard parameter set to obtain complex food webs that are not too large. The computation time increase at least quadratically with species number making it undesirable to have too large food webs when considering simulations on large spatial networks.

Competition modulation

Last in this section, we sketch the influence of different values for the competition modulation δ. Figure 4.5 shows example time series again. Competition decreases from top to bottom. Interestingly, in the first panel competition is so strong that one can clearly see the network structure build up at the beginning of the simulation. The species number slowly grows to the stationary value of around 22 species. The emerging food web structure is nevertheless still comparable to the food webs seen so far, only with slightly fewer species in the higher trophic layers. The reason lies in the basal layer. Basal species cannot become too similar because of competition. We see their body masses are stretched over quite some range. To obtain a sufficiently large biomass input a higher level species needs more than one prey in

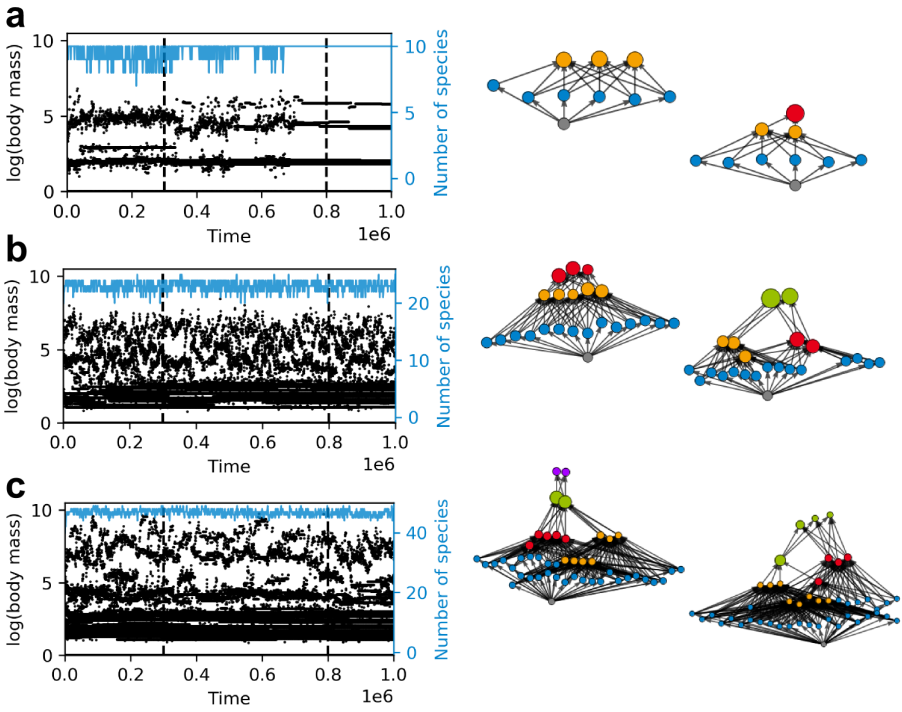

Fig. 4.2: Example timeseries for variation in R with λ = 0.65 and δ = 0.25. Resource size increases from top to bottom (**a**: 10, **b**: 50, **c**: 100). Left: Body mass time series, right: example networks for the points in time marked by the vertical lines in the time series. Number of species and number of trophic level (color coded; 1 = blue, 2 = yellow, 3 = red, 4 = green, 5 = purple) increase with R as more energy is available. The lowest layers become more crowded with increasing energy input.

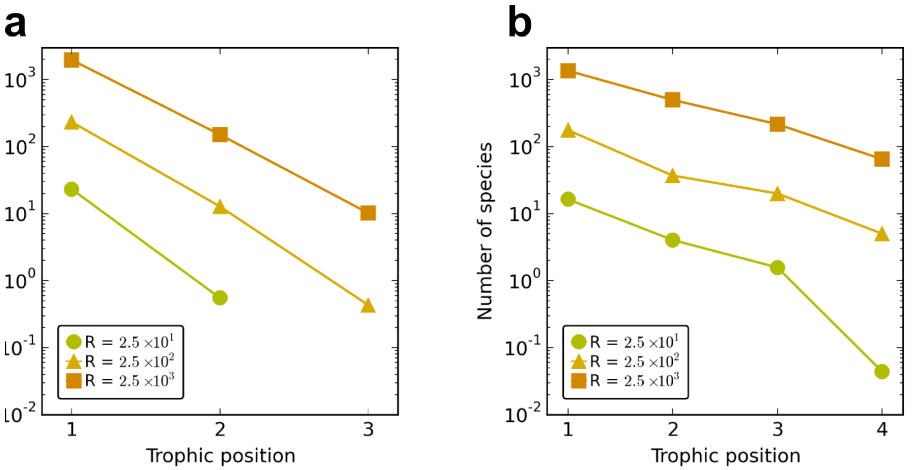

Fig. 4.3: Mean species per trophic level for increasing values of the resource R. **a**: Small efficiency $\lambda = 0.1$. The number of species per trophic level decreases fast. Larger resources shift the curve to higher number of species on all trophic layers. **b**: Large efficiency $\lambda = 0.65$. The decrease of species number with trophic layer is shallower compared to the small efficiency because more biomass can be allocated by the higher trophic layers.

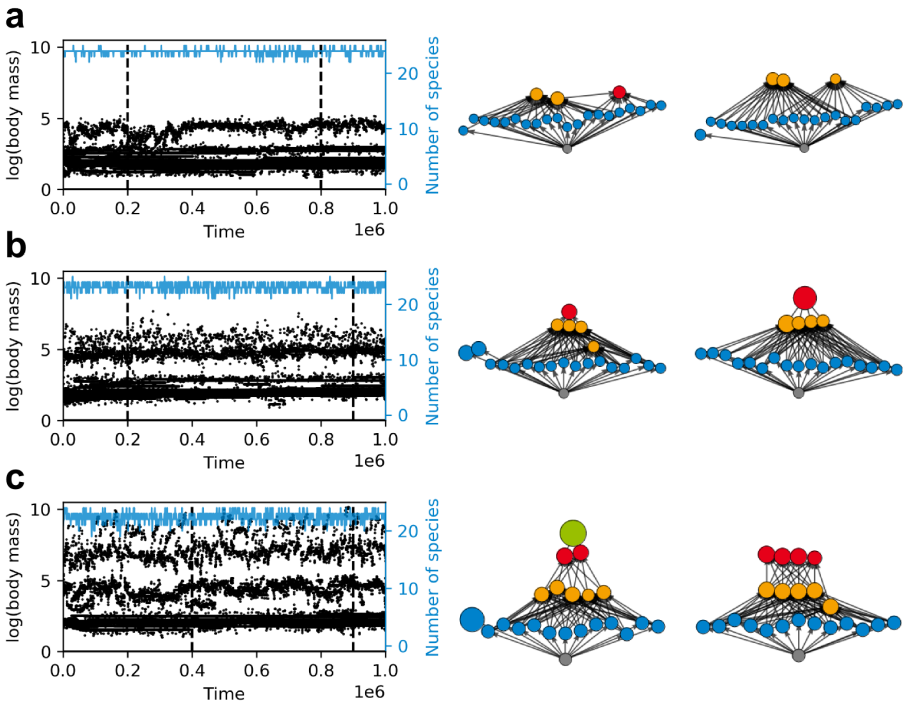

Fig. 4.4: Example time series for variation in λ with R = 25 and δ = 0.25. Efficiency λ increases from top to bottom (**a**: 0.2, **b**: 0.4, **c**: 0.8). Left: Body mass time series. Right: example networks for the points in time marked by the vertical lines in the time series. Species number stays constant, but the height of the food webs increases. For the highest efficiency even a forth trophic level (green) can be supported for some times. Small efficiency only allows for a crowded basal layer and few species above for this choice of R.

its feeding range. As feeding ranges are limited and competition between higher trophic species is also strong, only some consumers manage to have a large number of prey in their feeding ranges. Intermediate competition strength (in the range of the standard parameter) (middle panel) has a shorter build up phase, almost not visible in the time series, and leads to networks as we have seen in the standard parameter set with basal species that are more similar. Small competition means, that species can in principle become arbitrarily similar/different and still everyone gets the same share of the resource. The time series of small competition looks more blurred, than intermediate and high competition, indicating that trophic layers are indeed broken up, because prey is accepted equally no matter where in the feeding range it is located. This is also visible in the example networks.

Speciation Parameters

The speciation process is shaped by three parameters which determine how far the new body mass can lie away from the old one (q) and where the new feeding kernel is positioned with respect to the new species' body mass ($f_{\min}, f_{\max}$) as well as how wide feeding kernel can be ($s_{\min}, s_{\max}$).
Figure 4.6 shows exemplary variations for the interval from which the body mass is chosen during speciation. The parameter values used for panel a allows for smaller variation ($q = 0.5$). The resulting time series and example food webs show no difference to the standard parameter taking from [29]. Panel b in contrast shows a simulation with a larger variety ($q = 4$). Species are in this case distributed more evenly across the body mass scale. The clear trophic layered structure is blurred, but still discernable in the food web pictures. This occurs as new species have a wider range around the original body masses and thus chances are higher that a body mass in between two trophic levels is hit. Having a body mass outside of current trophic layers can be advantageous because of a lack of competitors. This leads to a faster change in the network structure as trophic layers move up and down.
Fig. 4.7 shows exemplary variation in the interval of the feeding center (a) and range (b). The feeding center interval is larger in the shown simulation (panel a). This leads to wider gaps between the trophic layers as species can now have prey with a way smaller body mass. Additionally, the body mass scale covered by a single trophic layer is larger because predator body mass can be further away from their prey's. Panel b shows a variety with a smaller feeding range allowed (between 0.1 and 0.5) in combination with the standard parameter for the feeding center. We observe that it takes the network way longer to build up around 20 species (blue curve) because newly introduced species have smaller chances of hitting a suitable

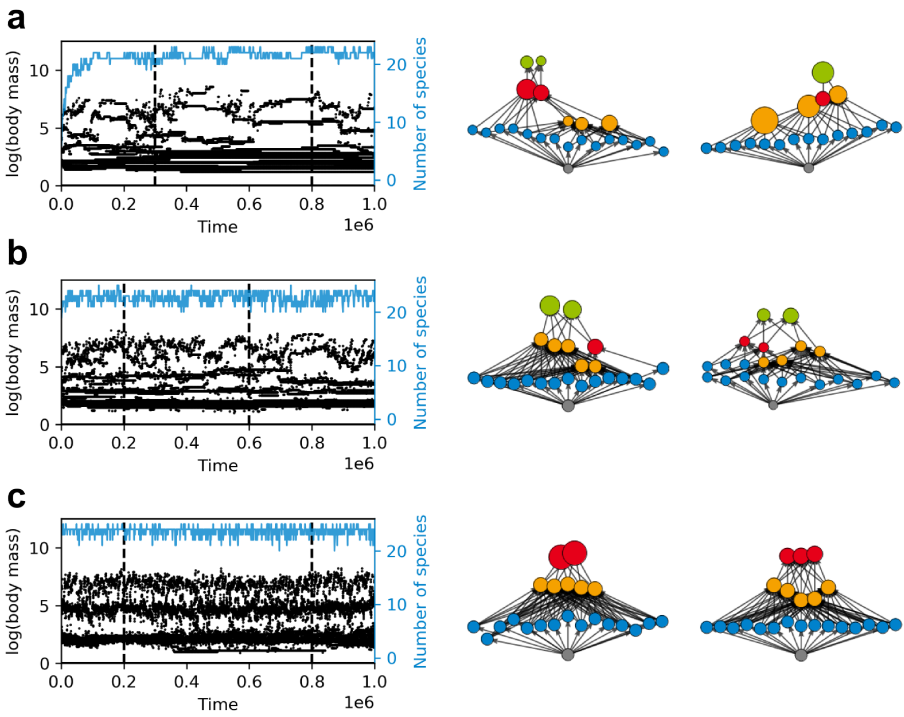

Fig. 4.5: Example time series for variation in δ with $R = 25$ and $\lambda = 0.65$. Competition strength decreases from top to bottom, i.e., the competition parameter increases (**a**: 0.001, **b**: 0.1, **c**: 10.0). Left: Body mass time series. Right: example networks for the points in time marked by the vertical lines in the time series. For weak competition (c) the trophic structure becomes blurred. Strong competition allows only for few species on the upper layers, whilst intermediate competition yields food webs with balanced trophic layers.

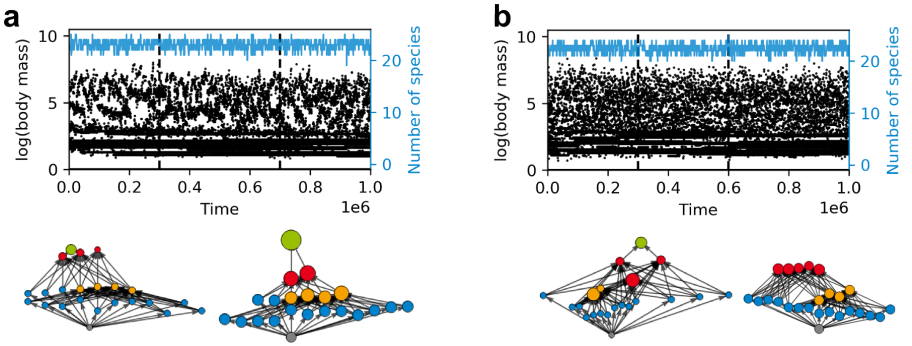

Fig. 4.6: Variation of body mass variance in speciation process. **a**: Smaller body mass variation in speciation events (q = 0.5). **b**: Larger body mass variation in speciation events (q = 4).

number of prey with a smaller feeding range. This is also illustrated in the network examples. Each species of the second trophic level (yellow) feeds on a subset of the basal species (blue) because the feeding range does not cover more of the body mass axis. The next trophic level has the same difficulties to overcome and can only establish if some prey species lie close together (right example) or one prey species happens to be in the small feeding range that has a biomass density large enough to support another layer.

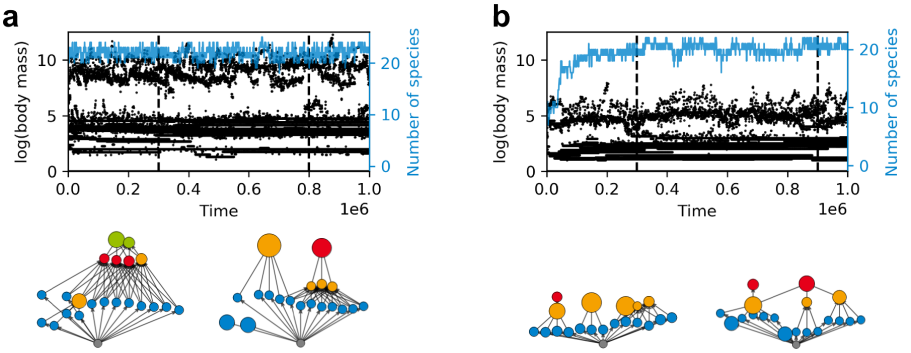

Fig. 4.7: Variation of feeding range intervals. **a**: Feeding center further below body mass ($f_{\text{min}} = 1$ and $f_{\text{max}} = 5$). Trophic layers shift further apart. **b**: Smaller feeding range (0.1 - 0.5). Trophic layers are closer together.

4.5 Discussion

Any model is always specifically tailored for a scientific quest. We wanted to build a model that is capable of simulating complex trophic structures on large numbers of coupled habitats. This chapter introduced a new allometric evolutionary food web model that uses the well-known self-consistent population equation from the Webworld model [27]. That makes the computation of network structure very fast, as long as the number of species is not too large. The simulations conducted with the standard parameter set presented here (table 4.1) only take minutes to be computed for around 10^6 speciation events. Scaling this to large spatial scales ($\sim 10^3$ habitats) is still computable, even if we consider larger dispersal rates that elongate the simulation time further.

Nevertheless, some assumptions deserve some discussion or justification. We start at the beginning, the first assumption of the model: Species are only characterised by three traits that are entangled. This seems to be in contradiction to the n-dimensional hypervolume that each species occupies in the picture of Hutchinson [47]. The Webworld model followed this idea quite closely, characterising species by a large vector of traits. Those traits can be interpreted in spanning the niche space, the score matrix then defining interactions in this space. However, one cannot draw clear (biological) conclusions from arbitrary traits only modelled by natural numbers, nor is it clear how many traits should be used to characterise a species. So it is equally plausible to define a small set of traits and use those for species definition, especially when the master trait is empirically so well-studied

and found to impact all kinds of ecological relationships and biological functions [77].

From the biomass density ratios obtained in our SAD curve, we expect that those show a larger ratio of largest to smallest abundance if we assume a higher dimensional niche-space. In an empirical study in grassland communities diversity and evenness were reported to decrease as niche dimensionality was reduced, by supplying limiting nutrients in a non-limiting amount, which means that the SAD curves of those systems were flatter.

The way resources are distributed in our model makes it a broken stick model (refer to chapter 2). As briefly discussed in chapter 2 the ratio between largest and smallest abundance depends on how the resource is 'broken', i.e., distributed, between species. In our model one prey that serves as a resource for its predators is split between all those predators. The competition function models how different the gain is. The efficiency models how large the fraction gained from one prey is. Among other factors (like the number of prey species a predator has) the interplay of these parameters tunes the shape of the SAD. But tuning and shaping the SAD was not our goal. As we do not want to reproduce real data sets it is enough for our purpose to have SAD curves that follow the overall empirical shape, which we demonstrated.

Turning to the choice of concrete values for parameter the numerical value for λ might need explanation. Originally λ was introduced as the efficiency of biomass transfer from one trophic level to the next (in Webworld). The empirical established value of 0.1 [168] is much smaller than the value we use in our simulations (0.65). The empirical value refers to biomass flux to the next trophic level. The Webworld model did not distinguish between biomass and biomass fluxes, although the use of the value for λ in equation (4.5) indicates that it can be rather interpreted as a flux equation. However, realistic determination of efficiency is a science of its own and needs to incorporate for example below-ground processes. The success of the model justifies the abstraction of such detailed processes and concrete choice of parameter values. As stated above, the main goal is to perform simulations with small, but complex trophic food webs. We thus take the "unrealistic" values of λ into account, as this leads to food webs that have several trophic levels, despite the relative small number of species.

The parameter study showed that the dynamics and the structure of the obtained food webs are very robust to concrete values of parameters. High robustness against changes in parameter values was also reported for the original Webworld model [27] as well as changes in the concrete species interaction rules [169]. The model of Rogge et al. [29] also found their model to be very robust against changes in parameter values. The model presented here unites the robustness of the former

models. Because of the clear interpretation of and a predictable effect of a change in each of the small number of parameters inherited from the Webworld model the model can be used to create food webs with a desired shape. We choose to work with complex, but rather small, food webs with several layers, but this does not have to be the goal of every inquiry.
The dynamics that the model produces show a constant species turn over. The food web structure stays roughly the same, while the participants change. This is remarkable, as in other models a frozen structure was reached after some time [29,160] and an external extinction rate had to be introduced to obtain an ongoing species turn over [29]. Our model demonstrates that food webs can have intrinsic ongoing dynamics and do not rely on abiotic background fluctuations. Similar, as we do not observe large extinction avalanches we conclude that mass extinctions as seen in the fossil record are rather driven by external triggers and not by dynamics in the food web itself.

4.6 Conclusion

This chapter has introduced a new and simple evolutionary food web model that is based on body mass and calculates biomass densities with the help of an equation from the literature, which makes computation very fast. The model produces food webs consisting of several trophic levels with, qualitatively, reasonable SAD curves. Remarkably, the resulting dynamics shows constant species turn over across all trophic levels. The emerging food web structures are robust to changes in all parameters. This indicates that the model captures the essential features needed to replicate those structures. We are thus armed with a model that is capable of tackling the challenging expedition into the jungle of macroecological patterns in time and space.

5 Macroecological Patterns in Homogeneous Space

The rates at which speciation, immigration and extinction operate, now and in the past, determine the diversity of species.

Michael L. Rosenzweig [12]

The following chapter presents the patterns obtained by the new evolutionary food web model in homogeneous space. This is the use case where the new model can fully show its strengths, i.e., fast computation of large spatial systems and long time intervals, despite consideration of full trophic interactions. Several patterns emerge simultaneously: a power-law like lifetime distribution and regional SAR, a decaying community similarity over distance, a range size distribution with most species occupying small ranges and triangular shaped range expansion curves. The trophic level has a crucial influence on the chances for spreading trough the network because basal species find resources everywhere, whilst higher trophic species depend on a suitable lower layer. We also find that lifetime and range are linearly correlated in contradiction to the Red Queen hypothesis. All these patterns emerge in a homogeneous spatial setting with the same conditions on all habitats. The network structure itself creates heterogeneity that leads to species diversity in space. This emphasizes the importance of trophic structure in modelling and understanding macroecological patterns.
The results of this chapter are presented together with the results of the last chapter in the article *The concerted emergence of well-known spatial and temporal ecological patterns in an evolutionary foodweb model in space* that was submitted to Scientific Reports with Barbara Drossel as co-author [157].

5.1 Introduction

As we have already seen in chapter 2, ecology, especially macroecology, is full of patterns that appear regularly across all kinds of taxa and scales. We introduced the most ubiquitous and placed them in two categories: spatial and temporal. Although some of these patterns are almost a century old (Arrhenius and Gleason

formulated the species-area relationships mathematically in the 20s of the last century [170, 171]), a synthesis of temporal and spatial patterns is not yet in sight, even though scientists agree on their interrelatedness (and have done so for a long time) [12]. Surprisingly few studies aim at studying spatial and temporal patterns together. One problem is that temporal patterns remain to be mostly studied by paleobiologists and knowledge transfer between ecological and paleological disciplines is often limited [107]. A rare example of a study concerned with space and time, though on ecological scale, is [172]. In ecology most theory exists on the relation between spatial patterns [22, 113] with the most studied patterns being the SAD and the SAR. The SAR is particularly interesting for conservation strategies as the paragraph on the SLOSS debate in chapter 2 sketched. A fundamental "rule" that predicts species number with area is welcomed from a conservational point of view, but SARs vary considerably between taxa and biomes even though the overall shape of the power-law is conserved [19]. Since the seminal work of Preston [102] in the 1960s, the relation between SAD and SAR was explored and a number of attempts of finding a "unifying theory" were published [22]. McGill compared six of those theories and extracted assumptions that all those models share [22]. He named three ingredients that should be enough to explain several spatial patterns (SAD, SAR, decay of similarity) at once:

(1) A skewed SAD (the empirical hollow curve shape),

(2) Individuals of one species are clumped in space,

(3) Individuals of different species are not spatially correlated.

The reason behind is that sampling such an individual distribution leads to said patterns. What remains unexplained are the rationales behind the shape of the geometric distribution of species in space and the ecological mechanisms behind. This leads us to the quote that introduces this chapter. The mechanisms behind diversity patterns have long been identified to be speciation, dispersal and extinction [12]. Models that are concerned with patterns in space often neglect speciation and extinction. It is clear that these models cannot be used to study temporal patterns. One successful counter example that takes into account extinction is the neutral model by Hubbell [23]. The neutral model successfully reproduces SAR, decay with similarity, etc., but, as already mentioned in chapter 2, it is highly debated as it neglects the deep-rooted niche space idea and is only valid for a species community consisting of similar species, e.g., trees. Recently, a non-neutral model (Lotka-Volterra competition model) was proposed, that reproduces the macroecological patterns as well [24]. Interestingly, the authors show that the three "ingredients" asserted by McGill naturally arose in their model

communities when those approached regional diversity equilibrium. This indicates that one might not need to put in those three facts, but they can also emerge when combining speciation, extinction and dispersal. What has not yet been taken into consideration by any study is the influence of trophic structure. As we have seen in chapter 3, trophic structure is important if we want to gain a comprehensive insight in ecological dynamics as species on different levels of the food web might experience very different surroundings. Therefore, we utilise the new evolutionary food web model from chapter 4 and analyse which kind of patterns emerge in space and time. In doing so we tackle two knowledge gaps at once: Interplay of spatial and temporal patterns and the inclusion of trophic structure in such models. We find a surprising variety of patterns appearing together within our framework. On top of that we will demonstrate that trophic structure should not be neglected. We find that trophic position crucially determines the dispersal success and the shape of the range evolution curve of a species which in turn is related to its lifetime.

Model Extension to Space

We will set up a two dimensional grid (regular square lattice) of habitats with periodic boundary conditions and let the evolutionary dynamics from chapter 4 run on all of these habitats. Additionally, we will allow dispersal between neighbouring habitats. Links between habitats are considered as bidirectional.

Dispersal

A dispersal event takes place between two adjacent habitats from the source to the destination habitat. On the source habitat a species is randomly determined (weighted with biomass density) that will disperse. The destination habitat is randomly chosen from all neighbours of the source habitat. The chosen species is then copied to the target habitat and the biomasses are re-evaluated taking into account the newcomer by applying equation (4.5). Note that this dispersal event differs from the dispersal event in chapter 3 where real biomass flows between habitats were recorded. Here, the biomass densities are only determined by the network structure so the dispersal event brings no specific amount of biomass into the habitat, but only the presence of a new species. The network structure is altered by this event and new biomass densities of all species arise.

The time scale of dispersal is assumed to be smaller than the evolutionary time scale. The frequency with which dispersal events will happen w.r.t speciation events is determined by a dispersal rate d. This will also be the parameter that we vary as we fix the speciation rate to be 1. A dispersal rate of $d = 10$ will, for example, translate into an average of ten dispersal events per habitat for one speciation event

on this habitat. This is implemented by defining the probability of the two possible events, speciation and dispersal, to be

$$p\,(\text{speciation}) = \frac{1}{1+d} \quad \text{and} \quad p\,(\text{dispersal}) = \frac{d}{1+d}. \tag{5.1}$$

Simulation procedure

At the beginning the spatial grid is initialised by placing the same starting species on all habitats as a seed for the evolutionary algorithm. Following the probabilities stated above it is determined which event happens (speciation or dispersal) and an arbitrary habitat is selected that will be the starting point of the event. On this habitat a species is determined randomly (chances weighted by biomass density) to undergo the event. In case of a speciation event the biomass densities are locally evaluated after introducing the new species. In case of a dispersal event a target habitat is chosen and biomass densities on the target habitat are evaluated after copying the disperser. This is repeated for a fixed number of times per habitat, for simulations presented here in the order of $10^4 - 10^5$ speciation events per habitat.

5.2 Patterns in Homogeneous Space

We now turn to the empirical patterns in space and time that the new model produces. Simulations were conducted with the standard parameter set presented in Tab. 4.1. The number of habitat varies between 20×20 and 40×40 habitats.

We evaluate species lifetimes and ranges. Species lifetimes denote the time interval between the first appearance of a species through speciation and the final extinction of a species on the last habitat that it inhabited, i.e., the time this species was present on at least one habitat. A species' range is measured as the number of occupied habitats. This is in line with the methods used in empirical studies of species ranges. If exact range measures are missing "occupancy" is considered a good proxy for range [110, 113] which is the number of occupied cells in a grid that is laid over the surface of the earth, for example, cells with edge sizes of 1°×1°(reffering to lati- and longitudinal degrees) [173]. Paleological range is often measured in number of locations a fossilised species was found [111]. Area in our study also refers to a number of habitats, but is independent of the species inhabiting those habitats. In empirical studies area is measured in some suitable unit of area like m^2 or in occupancy. For the SAR curves area is sampled in a nested way [95]. This means that all smaller areas are included in the larger areas, c.f. Fig. 5.1.

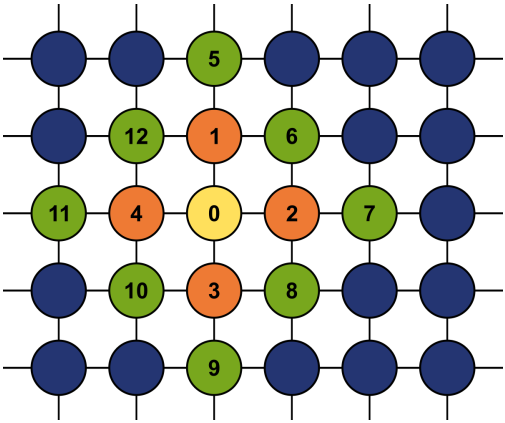

Fig. 5.1: Excerpt from a regular square lattice. The sampling procedure for the SAR analysis is illustrated by coloured nodes. The sampling starts at one arbitrary habitat (yellow, 0) for which species diversity is evaluated. For larger areas next neighbour habitats are added one after the other (arbitrary sequence indicated by numbers on the nodes) and species diversity on all these habitats together is evaluated (nested approach). As soon as all habitats that are one link away from the starting point are lumped into the sampling area the habitats that are two links away are considered. This procedure is repeated until all habitats have been considered, i.e., the whole area has been sampled.

Macroecological patterns

The results of the first simulation presented here were conducted on a grid with 40×40 habitats and varying dispersal rates. Simulations were run for 10^5 speciation events, on average, per habitat.

Lifetime distributions, see Figure 5.2a, show a power-law like behaviour for long lifetimes with an exponent around -2.4 (dashed line). This is considerable steeper than the empirical value [18] of -1.6 (dotted line) that also appeared in another model study [29]. The strength of dispersal barely influences the lifetime distribution. The SAR curves in contrast are affected by dispersal strength, see 5.2b. The overall shape of the curve is two-phased: For smaller areas a power-law like straight curve is observed that bends upwards to slope 1 (dotted line) for larger areas as expected for the continental scale [51]. For increasing dispersal rate the slopes get smaller. This is in agreement with previous findings [29, 174]. Stronger dispersal leads to larger ranges for species thus one needs to sample larger areas

to find the same amount of species compared to a case of weaker dispersal. As we have discussed in the theory part in Chapter 2, the SAR curve is expected to be triphasic. The curves obtained here do not show the first phase - the local scale. The local scale in empirical SARs comes from sampling on areas that are equal or smaller to species home ranges. This is a too small scale for our modelling approach to resolve. The food web approach used here starts with habitats that are assumed to hold a well-mixed composition of species. Thus it is expected that the SARs observed directly start in the regional scale.

Lifetime distributions and SARs were found to be entangled [29, 172]. In the system presented here the average range of a species increases linearly with lifetime (dashed line has slope 1). This is shown in 5.2c. For this graph species are binned logarithmically into small lifetime bins (bin size on log scale 0.055) and the corresponding range is obtained by averaging over the average ranges of all species in a lifetime bin. For ranges that are close to the system size at 1600 habitats the curve bends sub-linear away from the linear relation. Larger dispersal rates add a positive offset to the curve as it allows all species to spread further.

The lifetime distributions show that short lived species are the most numerous (c.f. Fig5.2a). Combining this observation with the linear relation of lifetime and range, range size distribution can be expected to show that a majority of species has small ranges. Figure 5.3a shows average and maximum range size distributions for a system with 400 habitats. Maximum range size is the maximum number of habitats a species once in its lifetime inhabited. We plot two curves: one for the basal layer, because they are most numerous, and one for all other species. As expected most species have small ranges and the distribution falls off for larger ranges quite steeply. For visual guidance we give a slope of -3 (dashed curve). Basal species more often occupy larger areas than species on higher trophic levels. A small fraction of basal species even manages to survive on average on all habitats. Those are the long-lived species when comparing with Fig. 5.2c. Only an even smaller fraction of non-basal species obtains at some point during their lifetime a range of the size of the grid (maximum range equal to system size). The main difference between basal and non-basal species is the ubiquity of their resource. Basal species find homogeneous conditions throughout the whole network while higher level species depend on a suitable layer of basal species to successfully invade a habitat.

Now it is clear that species ranges are small, but how are they distributed in space? To check community similarity we calculate the pairwise Jaccard index [42], i.e., the number of species present on both habitats divided by the combined number of distinct species of both habitats, for all combinations of habitats that have the same distance from each other averaged over ten equidistant points in time. Distance

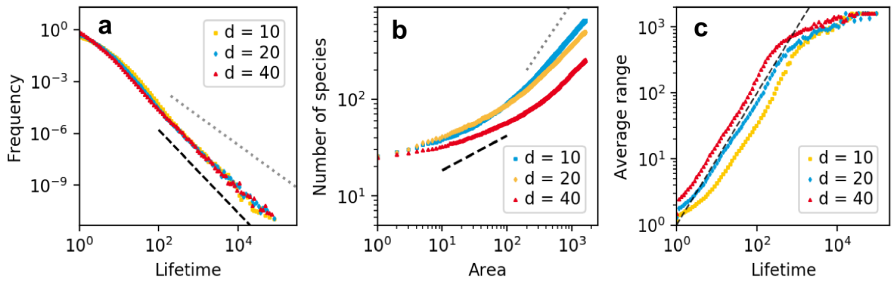

Fig. 5.2: (**a**) Lifetime distributions resemble power-laws for long lifetimes despite of dispersal rate. The exponent is around to -2.4 (black dashed), considerable steeper than empirical values around -1.6 (grey dotted). (**b**) SAR curves show two (regional, continental) of the three suggested phases with a power-law like shape in the regional range with empirical reasonable slopes (compare to black dashed empirical value of $z = 0.36$ [19]). The slope decreases with dispersal rate. The curves bend upwards towards $z = 1$ (grey dotted) as expected for the continental scale. The model cannot be used to simulate the local scale because of a too coarse resolution (food webs instead of individuals). (**c**) Relation between average area (number of habitats occupied during a species' lifetime) and lifetime is linear (dashed). Stronger dispersal leads to a positive offset in the curve.

is measured in number of hops from one habitat to the other. We then average similarity over all pairs and plot the resulting Jaccard index as a function of distance. Again, basal species are displayed separately. Similarity decays rapidly for non-basal species as expected from empirical studies. This indicates that species ranges are rather clumped or compact and not spread vastly. Basal species similarity decays way slower and settles around 0.8. This means that even 20 hops away 80% of the basal species are the same, indicating that there is a significant fraction of basal species on all habitats in network. Those are the species having large ranges and long lifetimes. The decay for small distances also indicates that basal species that are not yet spread far have clumped ranges. When relating this to the finding of the SAR the observation is in line with the small slope for small areas - neighbouring communities are similar because ranges are clumped, thus, sampling a small area leads to a number of species that is only slightly larger than the species number on a single habitat. This changes as soon as the sampled area is larger than typical range of species.

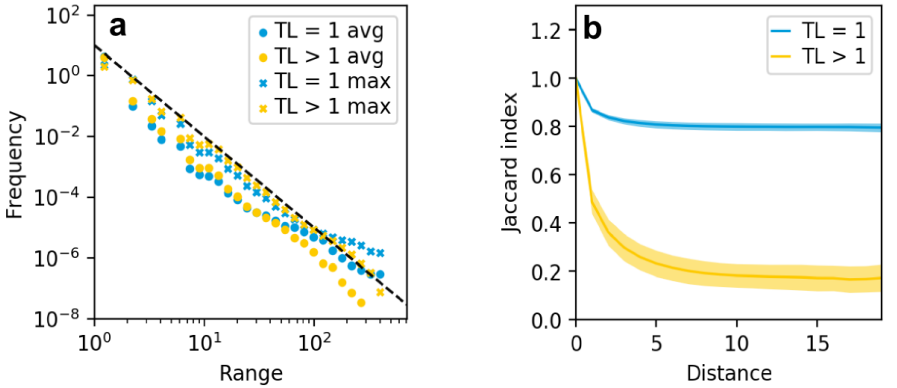

Fig. 5.3: (**a**) Average and maximum range distribution of species during a simulation in a 400 habitat system (dispersal rate d = 10) drawn separately for the basal layer (TL = 1) and all other species. The dashed line has a slope of -3, so range sizes are normally small. (**b**) Similarity of the communities expressed by the Jaccard index as a function of distance shows a decrease. Again we plot the curve for the basal layer separately, which decays less than non-basal similarity and settles at a similarity of around 0.8.

Geographic range size evolution

This section describes the results regarding the geographic range size evolution. This is no classical macroecological pattern like the RSD, because it appears on timescales much larger than what ecology usually takes into account and is concerned with only one speciess so it is rather a paleobiological pattern. However, as Rosenzweig pointed out, speciation, immigration and extinction determine the species diversity [12] this pattern must emerge by exactly these processes in concert with the other macroecological patterns. How does the geographic range evolve for single species? A compilation of range evolution curves is shown in Figure 5.4 for a simulation with 400 habitats and a dispersal strength of $d = 10$. The black curve refers to range whilst the blue curve shows the time series of the rank of this species averaged over all habitats. From top to bottom the trophic levels of the species increase as indicated by the arrow. Note that we only chose species that had a maximum range of at least half of the grid (200 out of 400 habitats). This is motivated by the fact that empirical species range studies will favour fossils that have large ranges because of a higher quality of the data sets. The time axis for each panel refers to the lifetime of each species, i.e., at $t = 0$ the species is derived

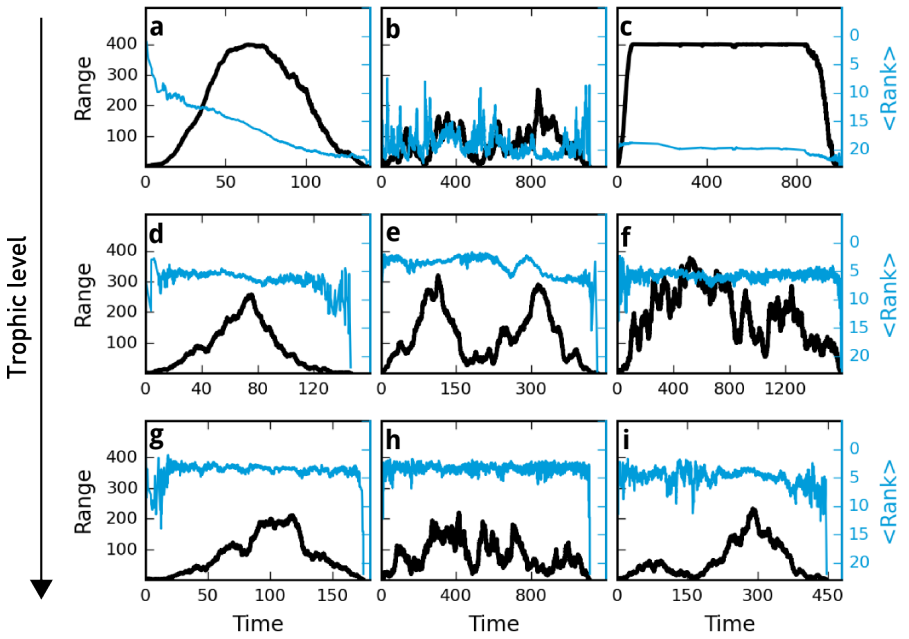

Fig. 5.4: Set of geographic range and rank expansion curves for different trophic levels increasing from top to bottom; (a-c) TL = 1; (d-f) TL = 2; (g-i) TL≥3. Diversity in range expansion curves increase with trophic level. Rank evolution cannot be used as an indicator for species fate, although in some cases rank decreases with lifetime indicating an "ageing" of the species.

somewhere from a speciation process and then spreads over the network. Note that time is measured in average number of speciation events per habitat, i.e., d dispersal events happen on average per speciation event per habitat.

The first observation is that geographic range of all species increases right after the species' creation. There is no "delayed" expansion, i.e., no species first resides on a small range and starts to broaden its range some time after the creation. The overall shapes that we observe of the range curves are twofold. A fraction of species shows a triangular shape of range expansion, i.e., a phase of expansion up to a point of maximum range followed by a phase of decreasing range up to the point of the species' extinction. The remaining fraction of species shows a wide range of differently shaped curves that cannot be easily sorted into categories. Some

curves look like random walks while others show two distinct triangular peaks, i.e., the species managed to escape extinction by starting a second range expansion. Interestingly, the triangular shape or "hat-pattern" appears often for basal species. Some basal species even manage to invade the whole network, as we have already seen above in the RSD, and show a long streched plateau at maximum range. Those species would spread further in a larger spatial grid and are thus also to be counted into the triangular shape category. Although the hat-shape also appears in curves for higher trophic level species those species experience more variety in their range expansion. Notably, the range curves also show that those species are on average distributed on a smaller number of habitats as already shown by the RSD curves, c.f. Fig. 5.3a.

The time series of the ranks fluctuate strongly. This indicates that species abundances vary largely between different habitats. Basal species seem to have a more even biomass abundance over their range as those show a steady decrease in rank over time for some examples. Such a signal might be used as an early warning sign for extinction risk, but is of course not reliable if it is not ubiquitously observed. Other mechanisms of early warning signalling are more promising, for example, by forecasting bifurcations from time series [175].

Overall basal species stand out from higher trophic species in their range and rank evolution as well as in the range size distribution and similarity decay. How can these differences between trophic levels be explained? The major difference between basal species and species on higher levels is the availability of food. Basal species see a homogeneous environment because the resource is available on all habitats in the same amount. In turn, a basal species that can survive in one habitat has high chances to survive in any other habitat (including neighbouring habitats) and survival chances should be limited mainly by competition. Non-basal species depend on the exact configuration of the basal layer. When they emerge locally through speciation they can persist because they match the local basal layer. If the basal layer changes in the surrounding landscape their traits will not help them to survive there. So species on higher trophic levels are not mainly driven by competition, but depend on the lower trophic layer(s). To quantify this expectations Figure 5.5 shows the extinction reasons for all trophic levels analysed for local events (speciation, shades of blue) and immigration events (shades of red), itemized for changes in the level above, below or in the same level (competition) as the species going extinct. Basal species show indeed that the top extinction cause is competition from incoming or locally emerging invaders. Non-basal species suffer particularly strong from changes in the lower level. The first consumer level (trophic level 2) has an even contribution from changes in the basal layer and competition in its extinction causes. But with increasing trophic position the combined

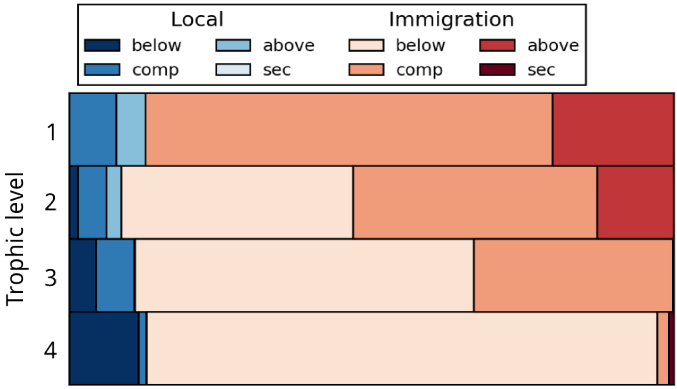

Fig. 5.5: Analysis of extinction reasons (fractions) per trophic level due to species arising locally (shades of blue) and species incoming from neighbouring habitats (shades of red). Additionally, distinguished are competition (incoming species has the same level as extinct species) and changes in the network on a level other than that of the extinct species. The top extinction cause for basal species is competition. Species on higher trophic levels are more often affected by changes in the trophic level below as they need these levels to prey on. Secondary extinctions due to extinction avalanches make only a tiny fraction in the reasons observed for species on the highest level 4.

influence from the layers below increases as changes from all lower levels might alter the network structure to the species' disadvantage.

5.3 Discussion

This chapter displayed the strength of the new evolutionary food web model that we introduced in chapter 4: The study of the emergence of macroecological patterns by the interplay of speciation, dispersal and extinction in complex trophic communities (food webs). The result is a remarkable accumulation of patterns that all emerge at the same time. On local scales we already discussed the SAD curves, see chapter 4. For larger spatial scales we find RSD that show that most species have small ranges and a decaying similarity with distance that indicates species are clumped in space. As a consequence we find a two-phased SAR with a power-law like regional scale that has empirical exponents. Lifetime distributions

follow a power-law steeper than expected from empirical findings and range expansion curves also show, besides various patterns, the triangular shaped pattern known from empirical data. Because every aspect of the model is known we can extract the underlying mechanisms.

The range patterns found agree with empirical findings insofar as most species have small ranges [88] and range expansion curves of a fraction of species resembles the well-known triangular shape. Our simulations revealed a novel result, namely the dependence on trophic level of range and range evolution curve. To this point no model was able to analyse these relationships because of a lack of trophic details. Non-basal species have smaller ranges and more diverse expansion curves as basal species, which often show a triangular expansion pattern.

Analysis of empirical data of basal mammal ranges tried to disentangle the influence of competition and environmental factors on the hat-shape [111]. As a result the authors found that environment was the main factor in the phase of early expansion and late decrease in range whilst the point in time when a species reaches the maximum range was more determined by competition. Theoretical simulations of random walks accompanying these empirical studies delivered realistic looking curves if they incorporated some form of competition and environment [111]. Relating these results with our findings on basal species, which often show those triangular shaped curves, enables us to identify mechanisms behind this pattern. Note that the environment in our case is not modelled explicitly, but emerges self-organized as the network structure in each habitat separately. Any species that can establish a local population after origination fits into the environment (and replaces an existing species because resources are limited). As the surrounding habitats are similar (as seen in Fig. 5.3b) the chances for a species are high that it will fit into these habitats as well, replacing an existing species. This leads to a phase of range expansion for this species as long as the neighbourhood stays similar. As soon as new species emerge locally that outcompete this old species the maximum range is reached and we are at “the tip of the triangle”. The old species becomes the inferior competitor and its range decreases as the new species is in the phase of expansion. This process repeats over and over again leading to a constant waxing and waning of species ranges between their origination and extinction. In our model competition rules the whole range process for basal species yet the curves look just like empirical ones. On the other hand the competition pressure is caused by the alteration of the network which in turn is a change in environment. The species does (not) fit the environment in the in-(de-)creasing phases due to competition. In summary, we observe dynamics that are comparable to the mechanisms proposed by Zliobaite et al. [111], but the important difference lies in the truly biotic interactions driving all the processes in our model and the lack of any abiotic interaction.

This should not deny the importance of abiotic factors, but rather emphasise the influence of trophic interactions. For example, a heterogeneous resource distribution will lead to different ranges and range curves which we discuss in the next chapter 6. In nature both factors, biotic and abiotic, will inevitably interact and shape the range expansion of a species together.

The range expansion for higher trophic species and a fraction of basal species did not show the clear hat pattern. The result that range expansion curves change shape with trophic level is new and empirically not studied as far as we know. As we have seen, the main difference between basal and non-basal species is their (in)-dependence of the lower trophic layer(s), which is reflected in the extinction causes. This may be interpreted as a stronger influence of the environment on these species. For consumers on trophic level 2 the advent of a new species can have two outcomes: either it is a new prey species which leads to a better availability of food, or it is a non-prey species which is a disadvantage for the consumer as resource is allocated in a part of the niche space that the consumer cannot reach. Thus a consumer might be rescued from extinction by an incoming new prey species or it might go extinct together with its prey (which is outcompeted by the newcomer). This already reflects the larger space of possibilities for a non-basal species, all which are not open for basal species. Comparison with empirical data is unfortunately impossible as we know of no study that deals with consumer range expansion explicitly. Most empirical studies revolve around basal species. This leads us to the conclusion that the "ubiquitous hat pattern" might not be so ubiquitous at all, particularly not for species that rely on specific food sources (in a broader sense this could also be any other resource). We hope that this result sparks interest in studying the range expansion on other trophic layers and paint a more comprehensive picture of range expansion in evolutionary time.

The impact of trophic level does not only manifest in the range expansion curves, but also in the range size distributions and most prominent in the distance decay of similarity. Basal species spread further than higher-level species and in turn show a smaller decrease with distance. This is in line with empirical findings on the relation of decay rates and trophic layer [90] that found carnivorous species to have a considerably steeper decay with distance than omni- and herbivores [90]. As we have sketched in chapter 2 the mechanisms invoked for explaining distance decay are either species sorting (environment has a heterogeneous substructure and thus presents a heterogeneous niche space where species can sort along according to their traits) or a dispersal centred view in which the environment presents differing dispersal obstacles for different species, depending on their dispersal abilities [16]. In both cases the environment plays a crucial role "painting the scene" in which species play. In our model we do not assume any heterogeneity in the environment

(uniform degree distribution and resource distribution) and assign all species more or less the same dispersal abilities, yet we observe the decay of similarity with distance. How can we interpret our results in the habitat heterogeneity framework? One may argue that basal species do sort along an environmental gradient, but as we choose a uniform one this leads to a quite homogeneous basal layer that is mirrored in a slow decay of the similarity of the basal layer. However, the basal layer *is not* identical on all habitats, as locally species emerge by speciation and keep the species turn over going by dispersing through the network. The basal layer thus creates an environment for the next trophic level that is more heterogeneous than what the basal species experience. This leads to a faster decay of similarity in the higher trophic level, in line with the habitat heterogeneity view of decaying similarity. This is in agreement with the smaller ranges of non-basal species. As their environment changes more rapidly as for basal species they cannot obtain a large range without running into habitats where food is scarce or non-existent.

The high similarity between neighbouring communities, mostly due to the similar basal layers, lead to SARs with empirical exponents [19] for the regional scale [51] even for moderate to small dispersal rates. Rogge et al. [29] found SAR curves with much larger exponents for a comparable model based on speciation, dispersal and extinction. So our model performs better regarding SAR exponents. In contrast, lifetime distribution exponents in our model are steeper (-2.4) than in the model of Rogge et al. (-1.67) [29]. Empirical values revolve around an exponent of -1.7 ± 0.3 [18] which is in better agreement with the results from Rogge et al. [29]. This value also appears in lifetime distributions that only span an ecological time scale [172, 176]. One important difference exists between the model of Rogge et al. [29] and the one presented here: The present model does not implement a random extinction event whilst Rogge et al. introduce a small chance of a random extinction for each species to prevent their food webs from running into a frozen configuration [29]. Random extinctions can be interpreted as disadvantageous environmental fluctuations that can in principle hit any species. Adding a rate like this to our model would shorten lifetimes even further. This can be related to an idea that McPeek formulated on lifetimes of species while studying lifetime distributions in a local evolutionary model [107]. Species are either save from extinction because they can truly coexist with their co-occurring species or moving towards extinction (transient species). But it is hard to determine which species is a transient as it can take a fairly long time for a species to finally become extinct. He argues that species are the longer in the transient phase the more similar they are to their competitors [107]. This implies that species in the networks of Rogge et al. are more similar than in our model. Both models use body mass, feeding rate and feeding center as traits, but our model uses Gaussian feeding kernels that

assign attack rates depending on the position of the prey inside the feeding kernel whilst Rogge et al. only use presence/absence feeding interactions [29]. In this relation our species are less similar and we expect to observe shorter lifetimes. All this discussion is to be taken with caution as there is no consensus on lifetimes having a power-law distribution. The distribution could also be exponential, as fossil data exhibits quite large uncertainties [18, 177]. An exponential would mean that an average lifetime could be defined, which is also possible in our model as our exponent of 2.4 is larger than 2.

An influential paper of McGill [22] tried to summarise what ingredients are necessary in a model to obtain spatial patterns of biodiversity (c.f. 2 and Section 5.1). He identified three: An SAD that is skewed to rare species (few abundant, many rare species), clumped species ranges and inter species locations being uncorrelated. In a recent study of an assembly model O'Sullivan et al. [24] found that these three ingredients emerge when their meta-assembly model was near regional equilibrium (SAD, RSD, uncorrelated species location). This model was designed to study ecological structural stability, i.e., the influence of the regional dynamics on the stability of communities. The trophic communities that our model produces operate at exactly that state (regional and local species equilibrium) where the proposed basic ingredients are most distinct. As discussed in chapter 4 we also observe skewed SADs and as we have seen in this chapter the ranges of species are clumped in space. We cannot say how the spatial correlation looks in our case, but as we studied trophic webs there will necessarily be some correlation of predators that are adapted to certain prey. Because we obtain such a large number of empirical patterns at once, including patterns that O'Sullivan et al. [24] did not analyse, such as lifetime distributions, we dare proclaiming that spatial de-correlation might not be the most important of the three basic ingredients proposed by McGill [22]. We are not the first authors to point this out, as May et al. [178] showed in a model that was designed to resemble the three basic ingredients by fitting it to empirical data of two different forests that this fitted model is able to predict the empirical SAR, but fails at similarity decay and correlation. The authors suggested that a non-correlation of species may be violated because of habitat preferences [178]. Habitat preferences can be interpreted in the model used here in a more drastic manner as habitat suitability. Species on higher trophic levels cannot choose any habitat but are restricted to habitats that hold prey.

5.4 Conclusion

We showed that our simple, spatially explicit, evolutionary food web model yields a whole set of macroecological patterns at once. This demonstrates that the interplay of speciation, dispersal and extinction is responsible for the patterns of diversity that are empirically observed. This is the first time that trophic structure was explicitly modelled in such a framework and the results show that trophic structure matters. Trophic level has a crucial impact on a species' perception of the world. The range expansion curves and the range sizes differ for basal and non-basal species because of different mechanisms that drive species turn over. Basal species are driven by competition whilst higher trophic species are driven by a combination of competition and bottom up effects. As hard as it is to include trophic structure in empirical studies as simple is it to include it in simulations now that we have an evolutionary model that is capable of running on a huge amount of patches. The fossil record is a sound but incomplete data base [104] and extinctions make it impossible to study those species as if they were alive [66]. Evolutionary food web models are able to produce a complete record of species and their properties. Consequently, this study advocates the application and further development of complex food web models in exploring the entanglements between temporal and spatial aspects and bring paleobiology and macroecology closer together.

6 Macroecological Patterns in Heterogeneous Space

We already studied the detailed influence of heterogeneity and ecotones in chapter 3, but that was done on ecological time scales alone. The evolutionary model studied in chapters 4 and 5 can be extended to a heterogeneous scenario by alteration of the spatial environment. This chapter sketches briefly how heterogeneity can be included and gives an overview how macroecological patterns change in such an environment. We find that the overall shape of most patterns stays the same, but range sizes of species get smaller which results in a faster decay of similarity and a higher number of species in total. Range size evolution curves differ compared to homogeneous systems. This chapter should be seen as a first exemplary step in exploring further powers of the model.

6.1 Introduction

The assumption of homogeneity is always a simplifying assumption. Heterogeneity is the norm at all spatial scales. On tiny to small spatial scales factors like microclimate crucially determine what living conditions will be in a certain spot. For example, the difference in average soil temperature in an North American oak dominated forest was as large as 2.5°C in a small plot of only 80×80 at the same day [179]. Another example is an insect herbivore living on a plant. Even if the leaves of the plant might look similar to an inattentive observer, plants often show large variety, e.g., in nutrient abundance in their leaves. Often younger leaves hold more nutrients but might at the same time be more defended (by chemicals or physical defence mechanisms) [180]. When going to larger scales it might seem to become easier to justify the homogeneity of an area because slightly different areas are well-mixed inside a larger plot if the area of interest does not encompass an ecotone. But looking at scales as large as continents climate zones will inevitably become a source of such intense heterogeneity that it cannot be ignored. Little wonder that the latitudinal gradient in diversity sparked the habitat heterogeneity hypothesis (recall chapter 2). The question remains if the observed forms of heterogeneity have an impact on the observed species distribution. It is probably a valid assumption to consider the mentioned oak forest as homogeneous for

bird diversity, despite variation in temperature, as bird composition will on average be similar in the forest (neglecting edges). But it will not be valid to assume the same forest to be considered homogeneous if for example the distribution in soil organisms depends on a gradient in pH value.
Reconsidering chapter 2, heterogeneity is remarkable often invoked in theoretical explanations of ecological patterns. For example, in the niche difference model for range size distributions or the application of the habitat heterogeneity hypothesis on SAR curves. In theory of ecotones heterogeneity is essential as a lack of heterogeneity would lead to a world without borders. But heterogeneity complicates things. This might be the most important factor why heterogeneity is often neglected or homogeneity is assumed for simplicity, similar to the situation of trophic interactions. Trophic interactions were successfully included in the new model so why should heterogeneity be left out?
We introduce heterogeneity in our model systems loosely based on meta-ecosystem theory. Meta-ecosystem theory arose as an extension of meta-community ecology to include abiotic factors, in principle merging meta-population and landscape ecology [181]. Species always depend on their environment and the environment is not uniform. With the development of meta-population theory the importance of dispersal was acknowledged, but there are more flows between habitats than just dispersing individuals. The carbon cycle moves immense amounts of matter all around the globe; the influx of material varying over eight orders of magnitude between sites [182]. The meta-ecosystem is in turn defined as "a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries" [181]. This emphasises the importance of energy flows that are not bound to the body of organisms like, for example, dead organic material that is passively transported by other organisms or streams (wind, water). We keep modelling ecosystems by food webs. The spatial surrounding will be changed from a regular homogeneous lattice into a heterogeneous random geometric graph. The next section explains the changes in detail.

6.2 Landscape Modification

We will create a heterogeneous environment to compare the results of the homogeneous environment of the last chapter with patterns emerging in heterogeneous landscapes.

Random geometric graphs

We will use random geometric graphs (RGGs) to model a heterogeneous environment. Our choice is mainly based on the aim to obtain a heterogeneous degree

distribution which we will use to determine the resource distribution (see next paragraph). An RGG is constructed by placing points (the nodes or habitats) randomly into an area (unit square) and connecting all points that are not further than a defined radius apart (Euclidean distance). Fig. 6.1 shows an example of such a graph. We will use periodic boundary conditions to omit effects at the edge of the area. This construction leads to non-uniform degree distributions which means that RGGs have a local structure [183] unlike the regular lattices that were used so far. The expected degree (mean degree) $\bar{d}$ depends on the chosen radius r as $\bar{d} = N\pi r^2$ where N is the number of nodes placed in the square. The radius can be used as a parameter to obtain an RGG with a desired mean degree

$$r = \sqrt{\frac{\bar{d}}{N\pi}}. \tag{6.1}$$

An RGG might not need be connected[6], but we will use only connected graphs in this chapter, i.e., there is a way from each habitat to each other habitat. For the implementation this means that RGGs are constructed and discarded if unconnected and the first RGG that is connected will be used as the underlying topology of the simulation. RGGs are structured by so called communities, i.e., groups of habitats are more connected to each other than to habitats outside of the community. This can be seen in the example graph, Fig. 6.1, by areas that have more dense lying nodes and areas that have only few nodes. Community detection in such graphs is a complicated algorithmic problem and various ways exist to find a mapping of nodes to communities [185] that is not the goal here. The only importance lies in the fact that there are local structures in RGGs. For the later results the degree of the habitats is most important. As degree is linked to the number of neighbours a habitat that is part of a large and well connected community is expected to have a higher degree than a habitat that lies outside of such a community.

Heterogeneous resource distribution

As the last section already adumbrated, flows through a network depend on the link distribution. When considering the meta-ecosystem idea this would mean that not only biomass in form of species moves or is transported between habitats, but also for example resources. Starting with a homogeneous resource distribution, so each habitat has the same amount of R/N resources, in an RGG with N habitats and assuming that a fixed fraction μ leaves each habitat equally distributed to all k_i neighbours (analogue to the patch-wise dispersal from literature [31, 33]) this

[6] The graph is with high probability connected if $r \geq (1+\epsilon)\sqrt{\frac{\lg N}{N\pi}}$, with $\epsilon > 0$ and with high probability has disconnected vertices if $r \leq (1-\epsilon)\sqrt{\frac{\lg N}{N\pi}}$ [184].

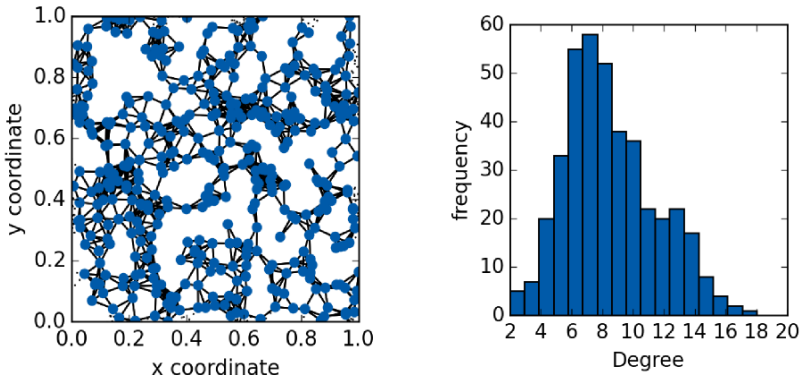

Fig. 6.1: Example of an RGG with 400 habitats with a radius of 0.056 (relating to a mean degree of 8). Dotted edges refer to edges drawn due to periodic boundary conditions. The corresponding degree distribution is shown on the right. Due to the restriction for graphs to be connected no nodes with a degree of 0 are allowed. The smallest degree in this example is 2.

leads to an outflow of resource $R_i^{\text{out}} = k_i \cdot \frac{\mu}{k_i} \cdot R_i$ in habitat i and an income of resource from all neighbours

$$R_i^{in} = \sum_{j=1}^{k^i} \frac{\mu R_j}{k_j} \tag{6.2}$$

where j runs over all neighbours. In equilibrium in and outflow need to balance each other out

$$k_i \cdot \frac{\mu}{k_i} \cdot R_i = \sum_{j=1}^{k^i} \frac{\mu R_j}{k_j}, \tag{6.3}$$

and with eliminating μ this yields

$$k^i \frac{R^i}{k^i} = \sum_{j=1}^{k^i} \frac{R^j}{k^j}. \tag{6.4}$$

This equation is solved for a constant flow on all links

$$\frac{R_j}{k_j} = \text{const.} \forall j \in [1, N] \tag{6.5}$$

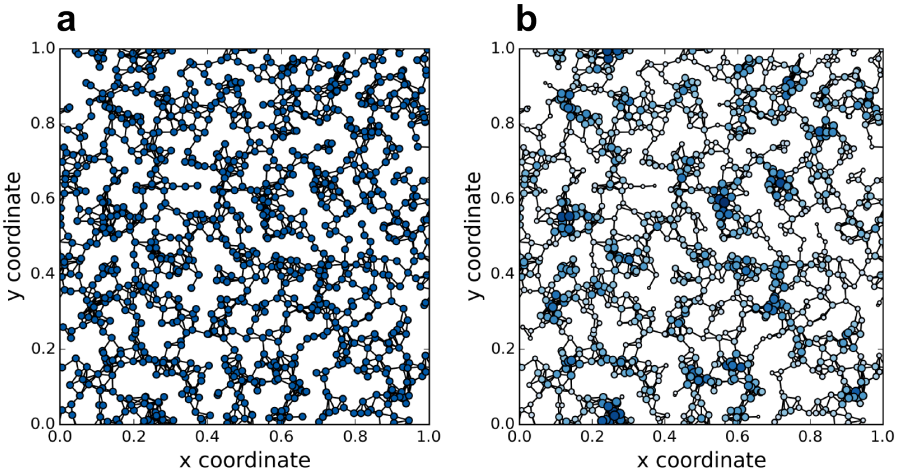

Fig. 6.2: Example of an RGG with a mean degree of 6. (a) Homogeneous resource distribution (all habitats have the same amount). (b) Resources distributed in accordance to node degree indicated by node size resembling the stationary state of resource flow assuming all links have the same weight.

which leads to a resource distribution that is proportional to the node degree

$$\frac{R_i}{R_j} = \frac{k_i}{k_j}. \tag{6.6}$$

The total amount of energy (sum of resources over all habitats) is conserved. Hence, the amount of energy per link is just the total resource divided by the total number of links L, i.e., $R_{\text{link}} = R/L = \text{const}$. A habitat with k_i links will then hold an amount of $k_i \cdot R_{\text{link}}$ resource. An example of this kind of resource distribution in shown in Fig. 6.2. Left is the RGG with a homogeneous resource distribution and right with a heterogeneous one indicated by scaling the node marker size with node degree.

Not all degree distributions are useful, though. As we have seen in chapter 4, the amount of energy per habitat determines the size of the network that can persist on this habitat. Heterogeneity (resource difference between habitats) must not be too large in order to keep a connected landscape. Otherwise habitats with only a few links will effectively "break" the connection to their neighbours because only a few basal species can exist there and dispersal of all other species must come to a halt when entering such habitats. We will show results for two different mean degrees, namely 6 and 10.

6.3 Patterns in Heterogeneous Space

We now turn to the patterns that we find in the heterogeneous landscapes and present them in the same order as in the last chapter. Fig. 6.3 shows lifetime distributions, SARs and lifetime-range relationships for two different resource distributions (differing in mean degree: top 6, bottom 10) in a system with 1000 habitats and different dispersal rates.

The lifetime distribution follows a fairly straight line in the log-log plot indicating a power-law like behaviour. The tail for longer lifetimes follows a slope around -2.4 (black dashed curve) just as in the homogeneous case. The shown variation in dispersal strength has no effect on the slope which is identical to the findings in the simulations on the regular lattice. The SAR curves are composed of two regimes, one for small to intermediate scales which follows a line in the log-log plot and another regime for larger scales where the curve bends towards steeper slopes. Those two phases were also observed in the homogeneous case. The slopes in the regional regime are in agreement with empirical expected values (black dashed curve $z = 0.36$ [19]). The overall impact of the dispersal rate is analogue to that in homogeneous systems, larger dispersal rate leads to flatter curves (smaller slopes). The regional regime extends to larger areas in the more heterogeneous system, in other words the SAR bends upwards into the continental scale at smaller areas in the system with a smaller mean degree. When comparing the end-points of the SAR curves one notices that less species are present in the system with a larger mean degree. This can be explained by the property of the RGGs to build communities. A larger mean degree leads to larger communities because the chances for each habitat to have more neighbours is increased. Habitats with many neighbours have large amounts of resources and can hold large food webs. Particularly, habitats in communities that have all roughly the same number of neighbours have similar resource abundances and thus can be considered more homogeneous. Habitats between such homogeneous communities that have little neighbours have small amounts of resource. Such habitats can only be inhabited by a few (in the limiting case basal) species and structure the landscape that higher trophic species experience. Those habitats are more frequent in graphs with a small mean degree. Effectively this leads to communities of similar species, with higher trophic species being "trapped" inside the communities. A higher degree is, thus, a re-homogenisation of the system as habitats with very few links are removed. A higher degree also decreases the system size effectively because a larger number of neighbours leads to a smaller diameter of the graph (see also Fig. 6.4). This is in line with a later branching off of the curve to the continental scale and a smaller number of species. Compared to the homogeneous SAR curves γ-diversity is larger in the heterogeneous system. The relation between range and lifetime is sub-linear,

unlike in the behaviour for the regular lattice. Still the trend stays that longer living species occupy larger ranges. Particularly for smaller lifetimes in the system with smaller mean degree, species tend to occupy smaller ranges than expected from a linear relation. The effect of the dispersal strength is identical to the observation in the grid, ranges are shifted towards larger values for stronger dispersal.
Fig. 6.4 shows the range distribution and similarity decay with distance for the two heterogeneous systems. The range distributions are separated by basal (blue) and non-basal species (yellow) as well as maximum (cross) and average (dot) range. The plot is in log-log scale and provides a slope of -3 for visual guidance. Most species have small ranges and ranges tend to be smaller than in the lattice, particularly for a small mean degree. The distribution falls off steeply for all displayed curves when going to larger ranges. Species on higher trophic layers have more often small ranges than basal species. Only a small fraction of species reaches ranges that are in the order of the size of the spatial system. We do not observe any species residing on average on all habitats as we did in the grid scenario (which was also for a smaller system size). But a non-negligible fraction of higher trophic species and an even higher fraction of basal species have a maximum range that is equal to the grid size, so at some point they were distributed across all habitats. The fraction of basal species with high maximum range is larger in the systems with larger mean degree, which also have overall slightly larger ranges for all species groups. According to the right panels in Fig. 6.4 similarity decreases with distance. The decay is particularly steep over the first few hops for the basal layer and then settles around 0.55. Higher trophic species similarity decays also rapidly and similarity falls even lower to a value below 0.2. Around the maximum distance of the graph similarity has a higher variability which is expected to smooth out for better statistics. The maximum distance is smaller for the system with a higher mean degree because habitats are coupled to more neighbours reducing the diameter of the graph. Neighbourhoods (communities) of habitats that are tightly coupled do not hold the exact same food webs due to different resource storage depending on their degree. On one hand, this results in the decline of community similarity for small distances. On the other hand, species that are on habitats with small resource supply have high chances of spreading to neighbouring habitats were resource supply is better. Thus, when the first distance is overcome it is likely that the next step is also possible which leads to a saturation in similarity. This value lies higher for basal species because they can in principle live on all habitats whilst higher level consumers cannot exist on habitats that either have too little resources allocated or no suitable prey species present. The further away from a habitat of interest the higher the chances that the biotic environment, i.e., the network structure, has changed considerably and in turn similarity keeps decreasing globally.

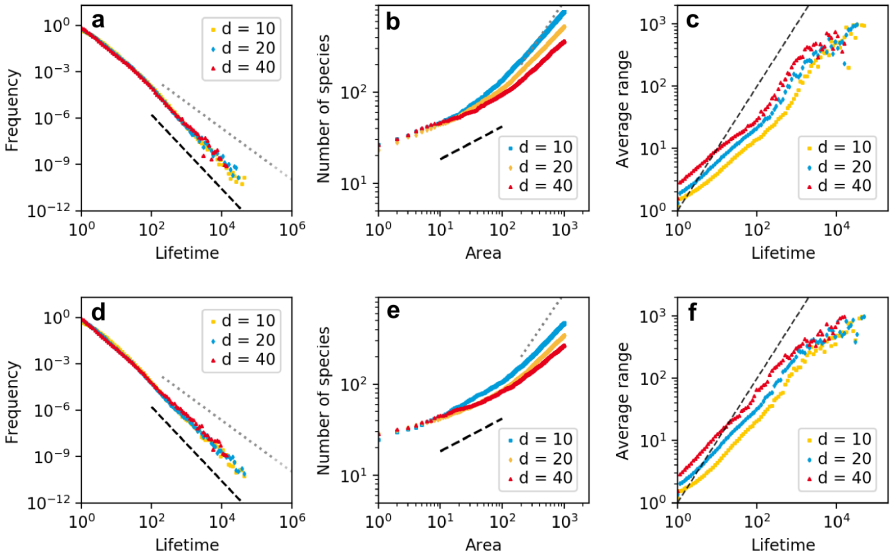

Fig. 6.3: Lifetime distribution, SAR and lifetime area relation for RGGs with **(a - c)** $\bar{d} = 6$ and **(d - f)** $\bar{d} = 10$. (**a, d**) Lifetime distributions resemble power laws for long lifetimes despite of the mean degree and dispersal strength. For visual guidance slopes of -2.4 (black dashed) and -1.67 (grey dotted) are shown. (**b, e**) SARs show the regional and the beginning of the continental phase (grey dotted slope of 1) of the empirical expectations (black dashed with slope 0.36) just like in the homogeneous case but with a larger γ-diversity than in homogeneous systems. Higher dispersal rates shift the curves to smaller slopes. Higher mean degree decreases system the size, resolving the regional scale on a finer grain. (**c, f**) Relation between average area and lifetime is sub-linear in contrast to the regular grid that showed a linear relation (dashed curve with slope 1). Stronger dispersal leads to a positive offset in the curve.

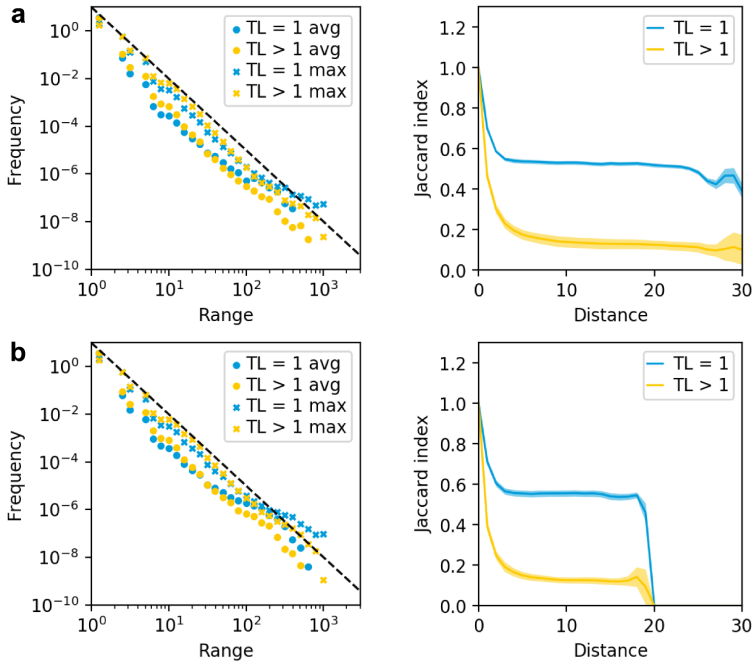

Fig. 6.4: Range distribution (right) and similarity (left) for RGGs with **a)** $\bar{d} = 6$ and **b)** $\bar{d} = 10$ for the simulations with 1000 habitats and a dispersal rate of $d = 10$. Range size distributions (left) show that species have small ranges. Ranges are slightly smaller in the system with smaller mean degree. The dashed curve gives a slope of -3 for orientation. A small fraction of species can spread to a large portion of the system. Similarity (right) decreases with distance. The maximum distance is smaller in the system with higher mean degree as habitats are on average connected to more neighbours.

Range expansion over time

The macroecological patterns seen so far showed only minor deviations from the homogeneous case. How does heterogeneity affect the concrete range expansion curves of single species?

Fig. 6.5 shows a selection of range expansion curves for species of basal and non-basal species (trophic level increases from top to bottom). The Simulation was conducted in a system with 400 habitats and a dispersal rate of $d = 10$. The x-axes span the lifetime of the shown species and measure time in average speciation events per habitat as before. Only species are considered that have at least spread across half of the habitats, 200 in this case.

Ranges start to grow as soon as species appear in the network. No species resides for a long time on a small number of habitats and starts to conquer the web afterwards. Range curves cannot be easily placed into the two categories (hat and non-hat) that were appropriate for homogeneous environments. Overall, the hat shape is only observed rarely for basal species. For basal species a new shape occurs frequently: the species spreads very fast on a large portion of the habitats and then range only declines very slowly and sometimes even in "steps", see, for example, in panels a and b of Fig. 6.5. This means that after a decrease in range the species resides for quite some time on all these habitats before loosing again a portion of range. This can again be explained by the internal structure of the random geometric graphs. As we have seen before, random geometric graphs show an internal community structure. A basal species that starts to conquer the network and is a superior competitor does not really experience this structure because it finds resource (even in small amounts) on all habitats. Because of ongoing local speciations new species will arise that cause extinctions. These species will first locally replace inferior competitors and need to have suitable traits to conquer neighbouring communities. An incoming competitor thus has high chances when invading one of the habitats of such a community to invade all of the habitats there. This can in turn be detected in a step down in the inferiors species' range curve. The trends in rank evolution of the basal species with the stairs pattern follow the range curve trends. Recalling the definition of the rank as the order of abundances we need to consider that ranks of habitats with different resource abundance cannot be compared easily. We show them nevertheless because the fluctuations are remarkably small and comparison seems possible despite differences in maximum rank on different habitats. Habitats with larger amount of resource offer more rank places (higher numbers in rank). This indicates that species showing the stairs pattern last longest on habitats with large amount of resource because of the high rank that they have before vanishing (blue curves in panels a,b). Panel c shows an example of a different rank evolution curve that is also frequently observed in the basal layer. This

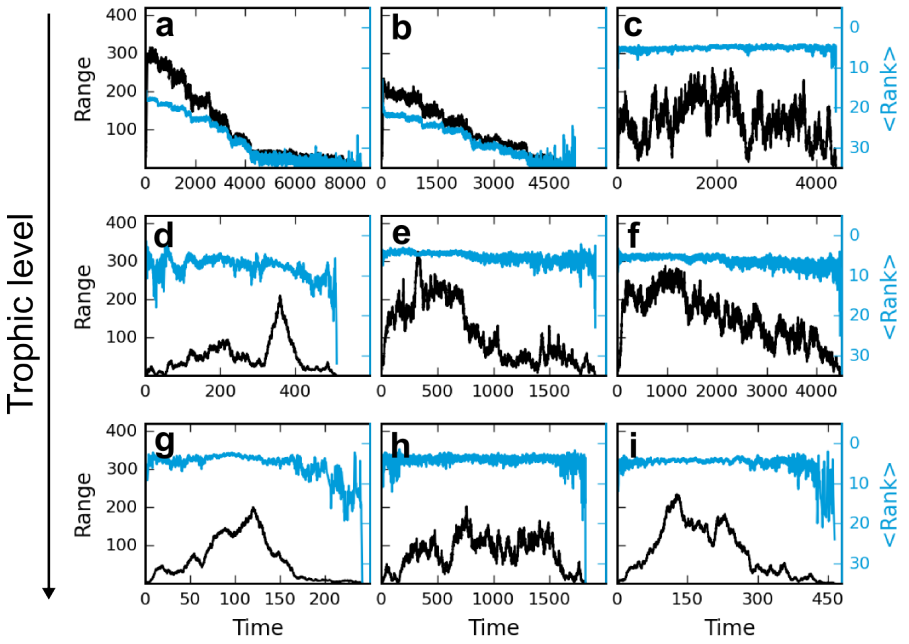

Fig. 6.5: Collection of range expansions for species living in a heterogeneous environment. Trophic level increases from top to bottom. Basal species show an elongated phase of decline in a step-like pattern, but the hat shape is not observed any more (**a-c**). Non-basal species show again diverse range expansion curves (**d-f**) also hat-like patterns that are observed most frequently in the species on the highest trophic level (**g-i**).

curve is a sequence of ups and downs in range, whilst rank is overall quite small, so the species is abundant. In this case, this particular basal species has a very small body mass and thus can avoid predation which leads to large abundances. As soon as a suitable predator appears the species range decreases and can increase again when the predator disappears.

For species higher in the food web the situation is different than for the basal species because they suffer from competition and depend on a sufficient basal layer on all habitats that they want to populate. The second aspect is emphasised by the heterogeneous resource distribution that leaves some habitats with small resource input allowing for less species on the higher levels. Species on trophic layer two

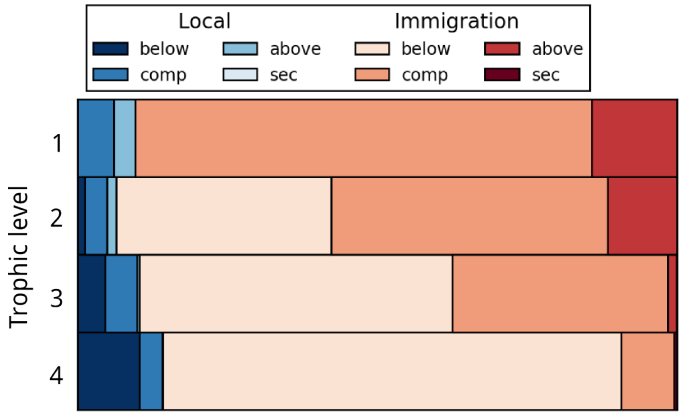

Fig. 6.6: Analysis of extinction reasons (fractions) per trophic level due to species arising locally (shades of blue) and species incoming from neighbouring habitats (shades of red). Additionally, distinguished are competition (incoming species has the same level as extinct species) and changes in the network on a level other than that of the extinct species. Like in the homogeneous system, species on higher trophic levels have two effects driving them extinct: Competition and changes in the network structure below, whilst basal species are competition driven.

(panels d-f) also show an elongated period of range decrease (e,f). This is in some cases also accompanied by large fluctuations (see panel f). Besides the case of elongated decrease other patterns appear that remind of the hat-pattern (d). This is especially visible in the species on higher levels (g-i, TL $\geq$ 3). The curves look similar to the range curves in the homogeneous case and resemble the hat pattern best of all trophic groups in the picture. This might indicate that the community like structure offers more stable and thus "homogeneous" conditions for the higher level trophic species. They might not be able to spread over the whole network, but the quality of their smaller ranges (communities) might be considered better.

For completeness we show again the contributions to extinction from possible changes in the network structure in Fig. 6.6. The composition of extinction reasons is analogue to the homogeneous case. Basal species are driven by competition whilst species on higher trophic levels suffer competition and changes in the lower trophic levels. The influence of network changes in lower levels increases with increasing trophic level.

6.4 Discussion

This chapter showed that most macroecological patterns keep their shape qualitatively when going to heterogeneous topologies and resource distributions. Those comprise lifetime distributions, SARs, RSDs and similarity decay, but range size evolution curves change considerably. Random geometric graphs have an internal structure of communities that is correlated to resource abundance in the construction used here. This leads to different dispersal success rates when dispersing inside a community or between communities. In turn, similarity decreases to lower values compared to homogeneous systems. Species range size evolution curves show a longer phase of decline because incoming invaders need to first manage to get into all the communities a species is dispersed over. The heterogeneous degree distribution alters the influence of dispersal among the habitats. Habitats with a large number of neighbours will more often receive incoming species from their surrounding than habitats that only have a small number of neighbours. Additionally, habitats with little resource cannot host large communities which can make them exclusive for species on lower trophic levels.

The results of the heterogeneous setting are compared to the results of the homogeneous systems in more detail. In explanations of the causes of diversity heterogeneity plays often a major role (see chapter 2). For example, the habitat heterogeneity hypothesis argues for more species in more diverse environments. Because of the concrete choice of our model we cannot resolve heterogeneity within a habitat, but only between habitats. Heterogeneity is introduced on a regional scale by the difference in resources between habitats and link distribution. We observe a larger γ-diversity in heterogeneous systems when comparing the end points of the SAR curves for homo- and heterogeneous systems (denote the different numbers of habitats; the homogeneous systems have even more habitats but less species). Recall that the average amount of resources per habitat is identical in both systems, only distributed differently. The reason lies in the smaller ranges species occupy, due to the heterogeneity that holds similar groups of species together in communities. Smaller ranges mean that more species can be distributed in the same number of habitats. Similarity decrease has also been proposed to decline faster with heterogeneity [16], which is exactly what we observe, and what must be the case when clumped ranges get smaller. Nevertheless, a fraction of basal species can persist on all habitats at least for some time of the simulation as in the homogeneous systems. For basal species the heterogeneity is not so strong because resource is still available in all habitats. In habitats where resource is less abundant, competition determines which of the basal species can persist. Those species then have traits that let them survive in all of the habitats.

One advantage of modelling space with an RGG is that it includes a spatial metric (Euclidean). This can be further exploited by modifying dispersal success depending on the real distance between habitats. Throughout this thesis, dispersal was not fined with any disadvantage. In the real world dispersal endeavours will come with some cost, be it a higher extinction probability or a weaker competition performance; the assumption that dispersal is free of deprivation does not hold. For example, the maintenance of organs that allow for dispersing fast and far is coupled to a higher energy demand [186].

Ryser et al. modelled a meta-food web in a landscape comprised of patches with heterogeneous degree distribution but homogeneous resource distribution with differing dispersal abilities between species on different trophic levels [187]. Larger bodied species (higher in the trophic network) could disperse further. They analysed how fragmentation affected the species composition by varying the connectivity in the landscape. The main result was that increasing isolation lead to fewer species in general and particularly reduced the number of higher trophic species [187]. The authors explained these results with a decrease in overall energy availability for more isolated compartments [187]. This is in line with our results of this chapter and chapter 5. Higher trophic species are more prone to extinction as they require large amounts of energy in a local site. With our choice of resource distribution habitats that are more isolated have less energy available, because influx is small. This makes it hard for higher trophic species to survive there. Differences in dispersal ability do not alter our results because the habitats cannot sustain large food webs on their own, so a higher influx of species is not able to keep a population over the extinction threshold.

This opens the discussion on the concrete modelling of heterogeneity in this chapter and how the results depend artificially on this choice. The idea is, as stated above, that energy flows between habitats under the assumption all links are equal. If one starts with a homogeneous distribution the energy will be distributed according to the degree of the vertices in equilibrium. We take it as confirmed that energy flows between places all over the earth [182]. The first simplification arises in the spatial structure we assume and in allowing flows only between neighbouring habitats. In a continuous real world especially passive dispersal can happen from nearly any site to any other if a suitable current is present. This means that sites can be connected that are fairly far apart and flow does not occur only into and from neighbouring habitats. For animal dispersal this is a fair assumption because they usually need to actively roam space and find routes into new areas, but other types of flows need different implementations of dispersal. Different dispersal rules can be applied in the framework used here. For passive dispersal, for example, a dispersal rate could be introduced that brings species into habitats that are further

apart; chances of dispersal scaling inversely with the distance squared or a similar function. The same rules apply to the resource flow. In principle, any form of energy flow can be implemented even temporal variation in flows or other not-stationary resource distributions that might be closer to real energy flows. As a starting point, however, a stationary resource distribution is desirable to keep track of all the processes going on in such a complex model. The strong dependence of food web height (maximum number of trophic layers) and resource pool size on a habitat can be regarded as a main point of criticism. Varying the resource pool between habitats thus immediately alters the possibilities for food webs to build up despite of any other concrete modelling choice like link distributions, etc. So one can argue that the observed effect of heterogeneity only lies in the sensitivity of the food web model. This is true indeed, but on the other hand this is in principle an implementation of a biological fact that food web height is determined by energy input [188]. The interesting part is the combination of a resource distribution and a spatial setting. The connection pattern of the habitats determines where habitats with low resource pools are located. Thus we see in our results the property of the random geometric graphs to form communities which are mirrored by larger trophic networks living on them because of higher amounts of resource. If this captures natural connectivity well or not is a matter of what system shall be described, as stated above. A drawback of the model lies in omitting dispersal as a biomass flow. Because the network structure alone determines the outcome of the biomasses and thus which species stays in a habitat the observation of source-sink dynamics, like in chapter 3, cannot be captured. It remains open how source-sink dynamics on evolutionary time scales affect the emerging patterns.

Regardless of the degree of realism in the modelling of heterogeneity, the model does give us insights on what results might be "exclusive" or more common to homogeneous systems. When comparing the range evolution curves for basal species in homogeneous (chapter 5) and heterogeneous systems, differences are remarkable, even though basal species do suffer least from changes in resource supply. The hat shape looses its prominence in the basal range curves and is replaced by a step-like decreasing function. We reason that these steps belong to communities in which a species is replaced in a short period of time. This indicates that hat shapes found in empirical studies of basal species might belong to species experiencing a homogeneous environment. The observation of hat-shaped patterns in higher trophic level species are in line with this statement if we interpret their restricted areas (communities) as more homogeneous because invaders first need to overcome the community border.

The consent on a triangular shape of range expansion has been pushed forward by empirical findings of this pattern in different taxa (e.g. mammals [189], marine in-

vertebrates [17], marine microorganisms [110]), but the abundance and quality in data varies considerably. The most apparent imbalance lies in the different number of studies concerning marine and terrestrial animals. Fossil data bases for marine animals are more complete and overall larger than for terrestrial animals. A quick search query in the Paleobiology Database (`paleobiodb.org`) delivers 127086 results for marine invertebrates and only 39783 for vertebrates, not even a third of the number of marine entries (retrieved November 2nd, 2019). Regarding range size evolution the studies that show symmetric range sizes most often belong to small, often basal, marine species, like invertebrates [17, 190]. We already mentioned that empirical data might be biased towards basal species and thus cannot predict range expansion for species on higher trophic layers. The results found in this chapter raise the question if empirical data may also be biased towards homogeneous environments or at least towards highly connected landscapes. One can speculate that marine environments may be the prototype of a highly connected and homogeneous environment and the focus on small organisms confines the results to species in low trophic layers. We do not want to stretch the interpretation of our results too far, but it should at least be mentioned that range expansion curves of terrestrial animals in disconnected landscapes might not develop their ranges in a strictly symmetric hat-like pattern.

Different shapes of the geographic range expansion curves have been proposed and possible underlying processes discussed in literature [109, 110]. A curve with an elongated phase of decline has been considered by Gaston [109] to fit his observations of extinction probabilities in birds, but a lack of empirical evidence due to a poor fossil record for birds cannot underpin this thesis [109]. Liow et al. analysed the waxing and waning in marine microfossils and found the waning phase to last longer than the waxing phase [110] which is in line with our findings in the heterogeneous systems. The difference in time spend between the two phases was not as strong as in our simulations, but rather around a 40-60 ratio, the concrete number depending on the data set [110]. The ratio in our simulations is highly shifted towards the decline phase. The phase of increase is so short for the basal species it is not even visible in the time series.

The elongated times of decrease in range might translate into a longer persistence time in highly isolated compartments because competitors arise more seldom. But we do not observe differences in lifetime distributions.

Another point that needs to be kept in mind is the different scales of taxonomy that are studied in paleobiological studies. Our study occurs on the species level. Often genera (higher taxonomic level than species) are studied, because better data sets are available. The comparison is thus not always straight forward, although for marine molluscs it has been shown that the difference between species and genus

level is small [17]. Again, this is an advantage for evolutionary models because empirical data on species level is scarcer, but one should also be aware of the differences when comparing the results.
The observation of differences in range expansion curves can further be compared to, at least for the waxing phase, contemporary range expansions of invasive species. An invasive species names a species that was introduced by human help (intentional or not) into a habitat where it originally did not occur and manages to spread through the new habitat. The American mink, originally from North America, is such an invasive species now found in Scotland. Minks escaped from several farms where they were kept for fur production and spread over the whole of Scotland [191]. The range expansion curves showed that minks spread with a constant rate in areas that can be considered as "suitable" for them and showed slower invasion success in less suitable areas like mountain tops [191]. The authors related this to habitat heterogeneity and concluded that in heterogeneous environments range expansion will occur with differing rates depending on the homogeneity of the transects that the invasion takes [191]. Another example reported constant invasion rates for the bank vole (a small rodent, also known as field mouse) in areas that can be considered homogeneous, but slowed invasion rates for areas that were disrupted by rivers or fragmented coast lines in Ireland [192]. In a nutshell, the increasing flank of the range expansion curves for these examples showed a steady increase with phases of stagnation in between whenever not-suitable areas were encountered. This supports the conclusion that a symmetric hat-like shaped range expansion curve appears in homogeneous environments. No statement can be made from invasive range expansion on the declining flank of the range curve. Caution must be taken because these processes occur on timescales much smaller than what the fossil record offers. However, the time resolution is much better and the exact environment of the species (geo- and biological) is known.
We claim that the exact form of terrestrial and especially higher trophic species range expansion in evolutionary time can be considered as unknown today because studies concerned with terrestrial animals have to deal with only a very limited number of data points [189], leaving space for interpretation of other patterns in those data sets. Our model can be used to analyse marine and terrestrial systems by using a corresponding spatial topology.

6.5 Conclusion

The habitat heterogeneity hypothesis was confirmed in the heterogeneous environments deployed here. Species ranges were smaller and in turn species diversity was larger without changing the overall shape of the SAR. Lifetime distribution was not affected by the changes in the underlying topology. Range evolution curves showed differences between trophic layers and the curves found in homogeneous systems. Our model does not only emphasise the impact of trophic layers on range evolution, but also rises questions of the impact of landscape connectivity or heterogeneity on range evolution. As long as fossil data remains scarce on range evolution of non-basal terrestrial species modelling approaches like the one used here can guide the search for sufficient data by indicating what curves might occur.

7 Conclusion

This work examined spatial and temporal patterns in macroecology by utilisation of several food web models. The first part was concerned with small spatial and temporal scales and analysed spatially coupled food webs with concrete population dynamics. Space was assumed to be heterogeneous with respect to resource availability. This allowed for two different spatial scenarios: Random heterogeneity and edges both realised by difference in the resource supply of habitats. Species diversity in the first scenario showed a hump-shaped dependence on dispersal strength confirming results that were obtained in previous studies in homogeneous spatial settings. Intermediate dispersal allowed for more species to persist in the system than in a comparable homogeneous system with the same total amount of resources due to source-sink dynamics between habitats of high and low resources. In a sense, the habitat heterogeneity hypothesis was shown to be dependent on dispersal. This means that heterogeneous landscapes do not per se hold more species, but that habitats need to be coupled sufficiently. Similarly, in the ecotone scenarios edge response was affected by dispersal strength and intermediate dispersal lead again to a positive edge behaviour because of the source-sink effect. This result can be used to extend existing frameworks on ecotone responses that rely only on resource distribution by dispersal strength.

The second part of this thesis took evolution explicitly into account. A new evolutionary food web model was introduced that combined species characterised by body mass and a well-established self-consisting equation for calculating biomasses from network structures [27]. This model has only a small number of parameters and produces food web structures that are quite robust to small changes in those parameter values. A speciation rule was defined to bring in new species and a constant species turn over was observed. The model did not run into a frozen state, nor did it show large extinction avalanches and produced complex networks with several trophic levels. The species abundance distributions resembled the empirical well-known pattern of a few abundant and many rare species, but with a relatively small difference between abundant and rare. Because of the simple biomass calculation the computational effort was small compared to models using differential equations. Consequently the new model was used to explore ecological patterns on large spatial and temporal scales.

First, a homogeneous spatial environment was assumed. Several patterns were found simultaneously in the simulations. Species lifetime distributions showed

power-law like tails with an exponent steeper than what empirical data suggests [18]. Species lifetime was correlated with range, a longer lifetime leading to a larger average range (or vice versa). Species were distributed in a clumped fashion with typically small ranges, leading to similar communities in the close neighbourhood and a decaying similarity with distance. Basal species were found to have larger ranges than higher trophic species because they benefit from the homogeneous environment which makes every habitat a suitable habitat for basal species. The species-area relationships were composed of two phases, a power-law like regional phase with slopes in empirical reasonable ranges and an upward curved regime for larger scales. Dispersal strength did not affect lifetimes, but lead to shallower SARs, because species ranges increased with dispersal strength. Range expansion curves often took hat-like shapes for basal species and more diverse forms for higher trophic species. The main difference between basal and non-basal species was the dependence of non-basal species on the lower network structure.

Second, the environment was modelled with a heterogeneous resource distribution that was constructed via the degree distribution of a random geometric graph, i.e., the amount of resource was proportional to a nodes degree. Random geometric graphs showed community building because resource distribution was coupled to degree. This led to resource rich communities that were loosely coupled to other communities. This had impacts on the patterns observed. Species ranges were smaller because of the resulting isolated communities, which lead to a stronger decline in similarity. The species-area relationships kept their shape, but showed a larger γ-diversity. Lifetime distributions were not affected. Range size curves were the most different patterns of all. The most striking feature was an elongated phase of range decline, particularly strong in basal species range curves. Comparing those curves to empirical data is difficult because there exists little to no literature on range expansion curves in terrestrial animals, which we think is best captured by our model. Most literature covers marine animals that can be assumed to live in rather homogeneous environments. The results from the model can serve as a starting point for examining how range expansion curves might look like in terrestrial fossils. Terrestrial species need to overcome more severe dispersal obstacles, like streams or mountains, which can be related to the communities occurring in the random geometric graphs.

The models used here make simplifying assumptions on complex ecological and paleological relations and processes. In the end a model is only an abstraction of reality, designed to study processes in isolation that might never occur under such circumstances. On one hand this makes models so wonderful, because they allow for exactly that isolated examination, on the other hand one must keep in mind the limitations and withstand the temptation of inferring too much from a model

to reality. In the end, the empiricist needs to measure nature as it truly is and hope remains that we will have at one point data sets that are large enough to answer all our questions. Contemporary means of gathering data, e.g., with satellites or microchips inside/on small species in symbiosis with an ever better technique of using huge amounts of data (so called "big data") enables empirical ecology to push the limit to ever growing spatial scales. Recently the number of trees has been estimated[7] on the scale of the earth compiling almost half a million data sets from ground sourced tree data [193]. Fossil data bases are growing and help completing the picture of ecology on ever growing temporal scales. But the ever growing stacks of data have little meaning if one does not know what to look for. Models like the models proposed here can indicate at what to look for and in which direction it might be interesting to dig deeper into the data mine, for example considering dispersal strength across ecotones that will definitely differ between species or consider the landscape structure in understanding geographic range expansion curves. An all-encompassing understanding of the processes forming the diverse life on earth will only be achieved by joining the forces of theory and empiricism.

[7] Apparently there are around 3 trillion trees on Earth [193].

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Wissenschaftlicher Werdegang

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Publikationen

- Michaela Hamm and Barbara Drossel, The Concerted Emergence of Macroecological Patterns in an Evolutionary Food Web Model in Space, submitted to *Scientific Reports*.

- Michaela Hamm and Barbara Drossel, Habitat Heterogeneity and Edge Effects in Model Metacommunities in *Journal of Theoretical Biology* (2017).

Lehrtätigkeit

WiSe 18/19	Betreuung von Studenten im Seminar „Reduktion und Emergenz in physikalischen Theorien“
SoSe 2018	Betreuung von Studenten im Seminar „Statistische Physik von Netzwerken“
WiSe 17/18	Übungsbetreuung Statistische Physik
SoSe 17	Betreuung von Studenten im Seminar „Statistische Physik von Netzwerken“
WiSe 16/17	Organisation der Übung Physik für Bauingenieure
2019	Betreuung der Bachelorarbeit von Kai-Luca Spanheimer
2015	Betreuung der Bachelorarbeit von Nadir Möller

Konferenzbeiträge

2018	DPG Frühjahrstagung, Berlin (Poster)
2017	Ecological Networks and Molecular Analysis of Trophic Interactions, Uppsala (Poster)
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